8—The Origin of the Tetrapods

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Introduction

In 1915 W. K. Gregory expressed the opinion that the Dipnoi and Crossopterygians were derived from a common ancestor. Since then palaentologists have shown an increasing tendency to regard the latter as the direct ancestors of the tetrapods. This belief is given very definite expression by Jarvik (1942) who derives the Urodela from one crossopterygian group, and the Anura from another.

In their recent contributions to the problem of the origin of the tetrapods palaentologists have devoted a great deal of attention to attempts to "restore" the soft anatomy of the fossils. In view of the fact that these highly speculative studies are receiving more than a passing recognition, a critical examination of the work seems to be called for.

The present contribution is divided into three sections. The first is an attempt to assess the value of the methods of the palaeontologists by applying them to recent forms. The second section is devoted to brief reviews of some of the contributions. The third presents evidence which, it is believed, indicates that the dawn of the tetrapods probably antedated the appearance of the Crossopterygia.

Section I
The Factual Evidence

This is, of course, provided by the fossils themselves. The skulls provide (1) dermal shield patterns, (2) neurocrania or neurocranial casts, (3) the bones of the palatoquadrate and (4) branchial skeleton. In addition, elements of the skeleton other than those of the head may be available for study, but these enter so little into phylogenetic studies that they may be neglected here.

(1) The Dermal Shield, when complete, is usually characteristic of the class to which the fossil belongs, and by comparison with these, the less complete specimens can, in the majority of instances, be identified with a good deal of confidence.

The value of the dermal shield patterns for phylogenetic studies may be tested by attempting to determine the natural classification of the recent forms on such evidence, and such a test throws the gravest doubt on their value. I have illustrated (Fig. 1) the dermal shields of several acanthopterygians. It is suggested that if these had been fossils it would not have been possible to recognise that they were closely related forms on this evidence. A very marked illustration of this unreliability of the dermal shield patterns is provided by those of *Accipenser* and *Polyodon* or *Psephurus*. There is no doubt that if we were to attempt the natural classification of the lower tetrapods and fishes on the evidence of their dermal shields, we should fail completely. *There is no reason for believing that the Dermal Shields of the fossils are any more reliable.*

(2) The Neurocrania and their attached sense capsules, like the dermal bones, are characteristic of the class to which the fossil belongs. Especially is this so if the boundaries of the component and covering bones can be determined. In the absence of these boundaries, or, in other words, if known from casts showing contours only, the specimen may not be readily identifiable. It is difficult to
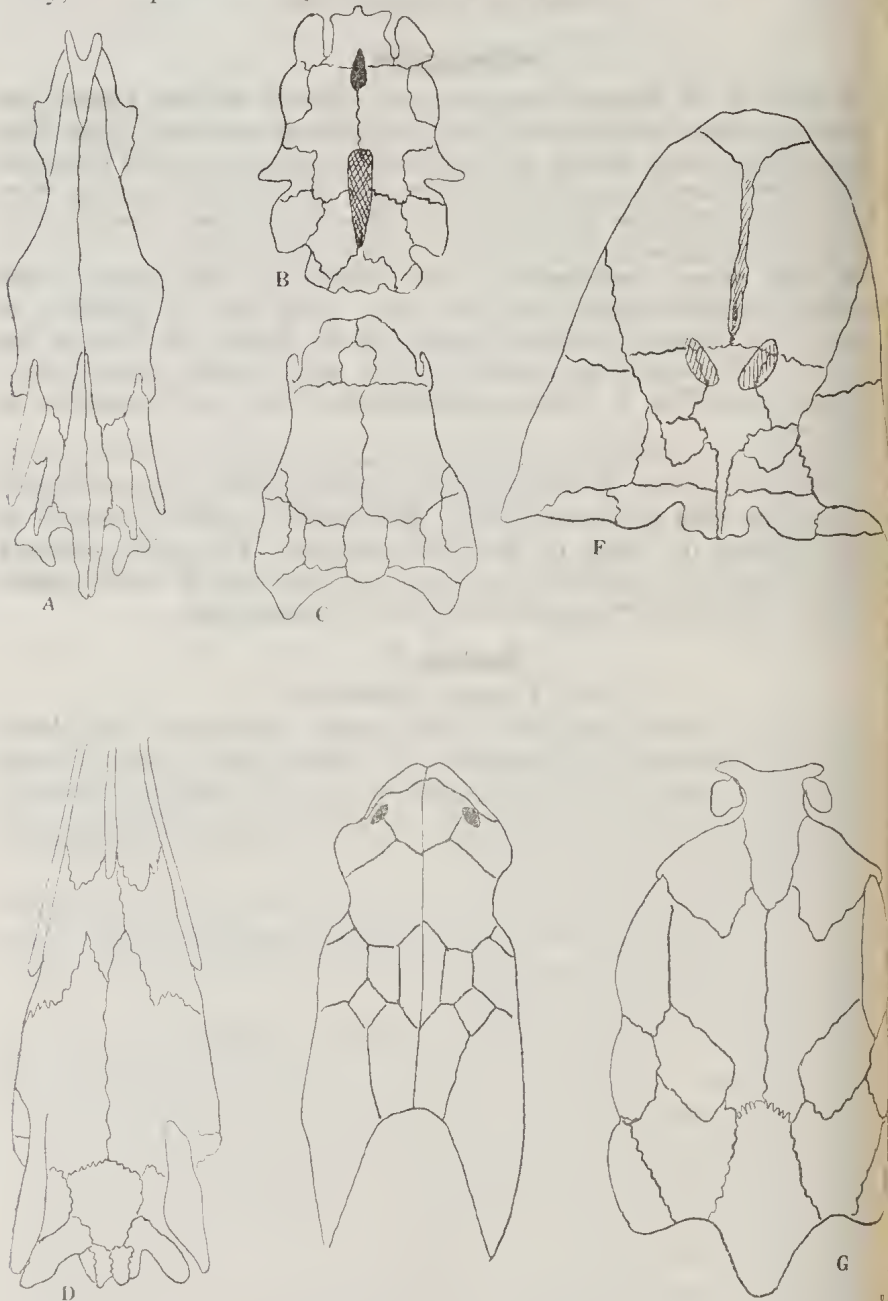

Fig. 1.—The Dermal Roof-patterns of seven Acanthopterygian fish. A. Luciolatus, Carpioides, C. Anabas, D. Istiophorus, E. Dactylopterus, F. Thunnus, G. Heterobranchus. (All from Gregory, 1933).

make comparison between the fossil material and the recent, because when the skull of a recent form is taken in hand, all the details of its architecture may be studied. It is probable, if the neurocranium of such a fish as *Tandanus* were found devoid of all suture lines between the bones, it would not be identified as that of the fish. The skull in question is platybasic, devoid of a myodome, and it is one of the very few fish in which the outer wall of the trigemino-facialis chamber is missing.

(3) The Bones of the Palato-quadrate are remarkably constant in number throughout the whole of the vertebrata, but they are very variable in degree of development and arrangement. Notwithstanding this variability, each arrangement is, in the majority of instances, characteristic of a particular class. In the fossil, as in the recent forms, these bones usually permit a ready recognition of the specimen, but, as with the dermal shield pattern, it would be quite impossible to arrive at a natural classification of the recent tetrapods and/or fishes on the evidence of the bones of the maxillo-palate alone.

When they are present along with the whole of the bones of the neurocranium, then, in the fossil specimens as with the recent, they may be used for phylogenetic studies, and with the same limitations. The limitations in question are those due to a lack of knowledge of the soft anatomy and embryology of the specimen. These limitations have been recognised by the palaeontologists, and they have attempted to "restore" or "reconstruct" the soft parts.

The Restorations

These have been devoted to attempts to visualise the brain, the constitution and distribution of the cranial nerves, the location of main blood vessels and the cephalic musculature.

(1) The Restoration of the Brains of the fossils has been carried out under the direction of two factors. The first of these is the shape of the cranial cavity, the second is the restorer's own belief as to what the brain should be like. The brains have been roughly fitted to the cavities, but their contours within the cavities have been determined by the affinities which the fossil was believed to exhibit. Thus, if the fossil, known to be a fish, was believed to show amphibian affinities, the detailed form of the brain was made to show similar affinities. The influence of this second factor was quite unavoidable. The mould of the cavity itself does not give any details of brain form, and these must, therefore, be filled in by the restorer. It is obvious that they cannot have been filled in haphazardly, the work had to be carried out according to plan, and this will, very certainly, have been dictated by the convictions of the restorer. In effect, the restoration is a pictorial presentation of the following statement:— The general form of the fossil indicates that it was probably allied to the class M. or N., and, therefore, its brain will have had the general form of that of the members of the group. All the detailed work which has gone into the restoration does not give it any greater value than this bald statement would have had.

Watson (1925, p. 848) wrote "the cerebral hemispheres, *if* we may judge from the character of the chamber in which they lay" were of a certain shape. The value of all these restorations of fossil

brains rests upon the correctness or otherwise of the assumption made in this sentence, and this is an assumption which may be tested by comparing the brains of recent lower tetrapods and fishes with the chambers in which they lay.

The mould of the cavities present in the neurocranium of *Paradicichthys venenatus,* Whiteley, is depicted below (Fig. 2A). This
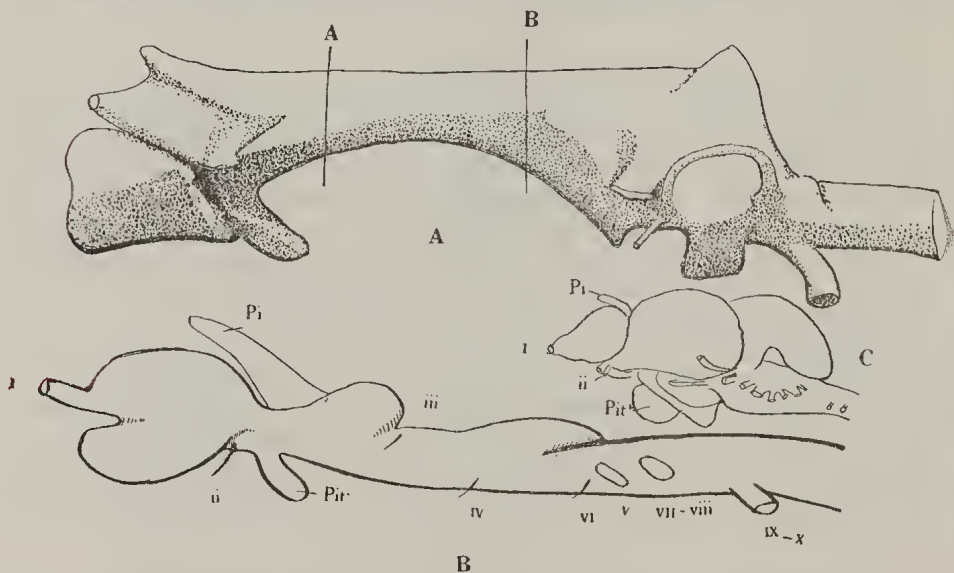

Fig. 2.—A. The cast of the cranial and ethmoidal cavities of *Paradicichthys venenata,* Whitley.
  B. A "restoration" of a brain to fit these cavities.
  C. The outline of a typical teleostean brain drawn to about the same scale. Pi. Pineal body. Pit. Pituitary body.

is a typical acanthopterygian, and the brain had the form shown (Fig. 2C). The mould recalled so strikingly that of *Megalichthys* that it was deemed worth while "restoring" a brain to fit it (Fig. 2B).

The next drawings present two views of the cast of the cavities in the neurocranium of *Amia,* and a "restoration" of the brain (Fig. 3).

In this case, as in that of *Paradicichthys,* all cartilage and connective tissue was removed before the mould was made, in order to reproduce conditions as they would be in a fossil.

The making of these moulds and their illustration may appear to some as a work of supererogation, because they illustrate a fact already well known to practical comparative anatomists, *viz.,* that the cranial cavity does not reflect the shape of the contained brain except in the theria. Not only is the mould of the cavities not like the contained brain, but it is very commonly very unlike it. This is due, of course, to the fact that the brains of the lower tetrapods do not nearly fill the cranial cavity, but are suspended, commonly well away from the walls, by loose, open-spongy connective tissue. In the case of the fossils, the moulds of the cranial cavities are likely to be even more misleading, because the cavity in many forms is limited by cartilage and/or connective tissue. If this had been so in the fossil, the cavity as found would be quite unlike that in which the brain was housed.

It is to be concluded that these "restorations" of the fossil brains may be quite unlike the original brain, and should not be regarded as other than pictorial expressions of opinion.

(2) The value of the restoration of the Constitution and Distribution of the Cranial Nerves and of the blood vessels of the fossils cannot be tested by attempting similar exercises with recent forms as the subject. The reason for this is that there could be no doubt about the identity of the specimen upon which the test is to be made. Provided the work was undertaken by a competent anatomist, it would
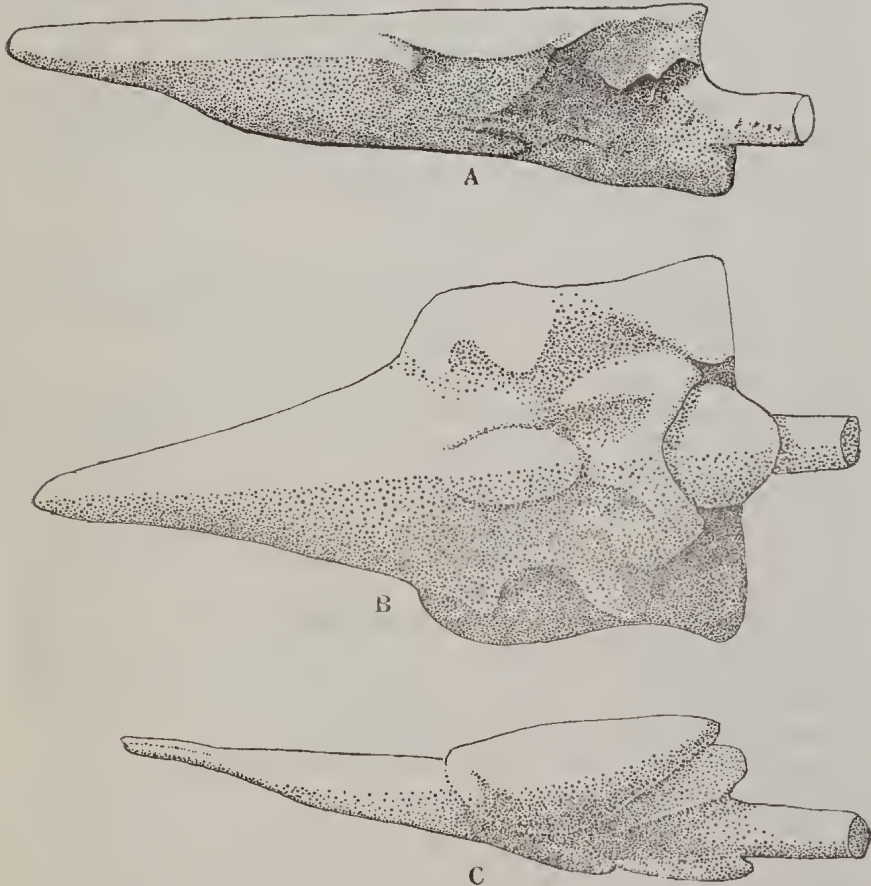

Fig. 3.—A. Lateral and B. ventral views of a cast of the cranial cavity of Amia. C. Lateral view of the brain as "restored" to fit the cavity.

be approximately correct in every instance. This very fact, however, throws grave doubts upon the value of such restorations in the case of the fossils. The work on the recent forms would be correct because the restoration would follow the well-known arrangement of the nerves and blood vessels in related forms. In fact, it would be dictated entirely by a knowledge of the anatomy of the other forms. In precisely the same way, the restoration of these things in the fossils has always been dictated by a knowledge of the anatomy in forms to which it is *believed* they were related. It would be quite impossible to attempt the restoration of the anatomy of a fossil except under such direction.

It follows that they are nothing more than detailed presentations of convictions as to the relation of the fossils to other forms — "Since this fossil appears to be related to M. or N., the distribution of its nerves and blood vessels was probably similar to that of those forms."

(3) The Restoration of the Cephalic Musculature may be undertaken with a good deal of confidence if the attempt is confined to the muscles of mastication. The skeleton will present the mechanical factors in the problem, and over and above this the actual points of origin and/or insertion are at times impressed upon the bones. Here again, however, one must be guided in the work by the number and general disposition of the muscles in related forms. If, for instance, the attempt were made to restore the muscles of a crocodile, under the impression that the specimen was an amphibian, the result would be quite astray from reality. On the other hand, assuming that it was a reptile, the result would, in the hands of a competent anatomist, approximate closely to actual conditions.

Once more the work must be directed by a knowledge or assumption of the class to which the fossil belongs. "Because this is a member of the group M. or N. the arrangement of its musculature was probably similar to that of the members of the group."

It is quite clear that these restorations are all very largely dictated by beliefs or convictions already held before they were undertaken. They are the result of convictions, and, therefore, should not be quoted as evidence in support thereof; they are not evidence at all, they are opinions. Too often in our endeavours to understand the way of evolution we are compelled, for want of definite evidence, to say, in effect or actually, "if this be true we may further assume." Although regrettable, this procedure is permissible so long as the "if" is properly recognised. When the argument continues:—in *fact* this cannot have been otherwise — it is neither permissible nor excusable. The second statement cannot be accepted as fact if based upon an assumption, and it should not be presented as such. I quote three examples of this reprehensible practice.

Watson (1925, p. 848): "the cerebral hemispheres, *if* we may judge from the character of the chamber in which they lay, were long and of considerable size. *In fact,* the brain as a whole cannot have differed greatly from that of Ceratodus or an amphibian."

Romer (1937, p. 34): "It is obvious that the brain as restored is essentially similar to that seen in dipnoans on the one hand and amphibians on the other; thus, the neurological evidence, as far as it goes, agrees with all other lines of work tending to indicate the close relationship of crossopterygians with the two groups. Of particular interest is the *fact* that the forebrain is here highly invaginated as in the amphibians — — ."

Jarvik (1942, p. 489) states that there are very considerable differences between the snouts of the Osteolepiformes and the Porolepiformes, and then proceeds to detail these in twenty-six numbered paragraphs. All are given as statements of fact. Of the twenty-six features, seventeen are based upon an assumption, they are restorations.

Section II

My criticism of some of the Palaeontological contributions is couched in emphatic language; to some it may appear unduly blunt. No apology is offered for the language used, but some explanation of it is certainly called for.

In effect, it has been stated again and again that our palaeontological colleagues have deliberately distorted facts to make them fit their theories on the origin of the Tetrapods. "Deliberate distortion" is usually a dishonest procedure; in this case it is most emphatically not so regarded, and it is sincerely hoped that such an implication will not be read into the arguments presented.

The convictions of our palaeontological colleagues are very real to them, and under the drive of these convictions they have quite honestly contended for their theories. The colour-blind man sees the scarlet robe and the green lawn the same colour, to him they *are* the same colour, but he is wrong. The Physicists have proven him so. Just so, it is argued in these pages, the palaeontologists, blinded by the early workers, are wrong.

Before proceeding to discussion of some of the individual contributions, some further general criticism of the whole of them may be offered.

Palaeontologists have, each of them, a faith in the correctness and reliability of their restorations and interpretations of the fossils which is not justified by experience. In support of this it may be pointed out that specimens have been studied by thoroughly competent palaeontologists, and later the same specimens have been studied by other, equally well-qualified, palaeontologists and each later student has decided that his predecessor was at fault in his interpretation and/or reconstruction. Perhaps one of the most striking examples of this sort of thing is provided by the following extract from D. M. S. Watson's Croonian Lecture (p. 234). "The neutral cranium of the osteolepids was first, though quite inadequately described by Rohon, later, and again misleadingly, by myself and H. Day and by E. A. Anderson, and finally and more successfully by W. L. Bryant. Dr. Bryant's description is, as Dr. Stensiö informs me, and as I have been able to confirm, from an examination of the original material, inaccurate in certain respects." That was in 1926, and Watson used the then accepted interpretation in his work on the evolution of the Amphibia. On top of all this examination and re-examination, in 1936, one of the specimens studied by Watson and Day was examined by Säve-Söderbergh and he writes (1936, p. 137), "By means of our modern technical outfit I was able to clean out perfectly the dorsal and lateral, and part of the ventral, surfaces of the neutral endocranium of this specimen, and to demonstrate a number of interesting points, which partly also change the interpretation of *Osteolepis* and *Eusthenopteron*."

The next general criticism which one feels impelled to make is to the effect that their work at times exhibits an unjustifiable degree of originality. The reference here is to the interpretation of foramina and grooves which they find on the fossils. Those who have had experience in actual dissection know that the identification of any but

the main nerve and vascular foramina cannot be attempted, and that, except at and close to the points of egress from the cranium, these structures are only exceptionally in contact with bone at all. Whilst sorry to speak so strongly as to offend or to risk giving offence, one cannot refrain from stating that these claims — to be able to determine the course and even the constitution of nerves and the number of cranial roots they had — must appear to be little short of ridiculous to all who have spent years in the laborious study of those things with scalpel and microtome.

As a matter of sober fact, the most that could be said on being presented with a skull, recent or fossil, complete or fragmentary, not being one which had been studied in the flesh, or which has been worked out by another investigator, is that — this is a fish, or perhaps an amphibian skull and therefore its nerve distribution and vascular arrangement were probably similar to the condition found in some related form. Although this is so, statements like the following are not uncommon. "The seventh nerve arises by a single root, so far as can be seen from the skull" (Watson, 1925, p. 845). To the student of the anatomy of living animals, statements like this are just fatuous. It is well known that the number of roots a nerve may have is never indicated on the skull, nor could it be.

Most palaeontologists, in their evolutionary equations, give too high a value to the factor provided by the arrangement of the dermal roof bones. It is fully realised that this criticism is founded to a large extent on the personal attitude; in other words, this is a matter of opinion and not, like the last, a statement founded on facts. One of the most outstanding of the latest contributions which base a classification of the vertebrata largely upon a possible chain of changes in the dermal roof bones is that of Säve-Söderbergh (1934-1936). Doubt as to the value of his evidence is centred in the fact that so many different roof patterns are presented by closely-related animals.

The Dipnoi alone present a whole series of such patterns. In order to base any scheme of evolution on the roof patterns, one has to *select* the examples of fishes and tetrapods, and to neglect the patterns of a number greater than that used in the comparisons. The marked variability in the dermal roof pattern has always appeared as evidence that those bones were, and in the living Teleostei still are, unstable and subject to non-significant variation. In short, it appears true to say that, amongst the fishes, there is no uniform plan of dermal roof pattern. It is as easy to select examples which would provide a chain of changes leading to the tetrapod pattern from the living teleosts as from the Crossopterygians. A selection of patterns drawn from modern fishes has been illustrated (fig. 1), and it was suggested that if these had been fossils, it would not have been possible to decide that they were really closely related forms, on this evidence.

It is submitted that the evidence points to the conclusion that the dermal roofing bones of the fishes are still in a condition of flux. If that be so, then it is further submitted that this is evidence which should lead us to expect that the roofing pattern was in at least as unstable a stage of evolution in devonian times as it is to-day.

It will probably have been noted that Säve-Söderbergh was unable to make use of Goodrich's careful analysis (1930) of the evidence and determination of a fundamental pattern in his last essay.

Säve-Söderbergh's concept of the composition of the dermal roof of the common ancestor of the Crossopterygians and Stegocephalians is apparently in the nature of an addition sum. It appears that he has listed all the bones found in the many fossils and endowed the hypothetical ancestor with the lot. He then proceeds to argue from this hypothesis as though it were a statement of fact. Unfortunately, no fossil is known which possessed the full list.

Far from his hypothesis being a statement of fact, it is arguable, on the evidence of the paucity of the number of bones in the *most* primitive fish forms known (the Arthrodira and the Antiarchi) and the wide diversity of the patterns in the *less* primitive, that these *latter* patterns have risen independently, and that there was no general plan from which they were evolved. If, however, we grant that Säve-Söderbergh's hypothesis is sound, we may also accept his following statement, which was that each of the many elements may alternatively have — (1) remained unchanged, (2) become fused with other elements, (3) become secondarily subdivided, or (4) reduced even to extinction. It is just the possibility of all these alternatives which detracts from the value of speculation on the assumption that any one or more of them has brought about the particular pattern derived. That there have been instances of persistence and of all three modes of change there is little reason to doubt, but there is nothing to guide us in determining whether reduction in number was due to deletion or fusion. True, when we find reduction in the number of a transverse row, we are justified, on the parallel of embryological evidence, in concluding that the bone which, in the more numerous row lodged the lateral line organ, has persisted. Whether the other has been lost by deletion or fusion will still remain for choice by the personal belief alone. It is the constant and unavoidable intrusion of this personal factor which makes all these theories unconvincing.

Säve-Söderbergh and Stensiö are agreed that reductions in number have, in the great majority of the instances, been due to fusions. In support of this belief, the former asserts that modern embryological investigations ("Pehrson, 1922, and others") have confirmed the views of Stensiö "in this respect." Watson, on the other hand (1921), states his belief that the reductions were due to deletions.

Pehrson demonstrated that the dermal roofing bones of *Amia* were developed by the fusion of more than one centre. This is probably the evidence referred to by Säve-Söderbergh. An analysis of Pehrson's work reveals the fact that the roofing bones of *Amia* are developed by the fusion of at least forty-two centres. Now, if these are of phylogenetic significance, in the way suggested by the reference, the forty-two centres should represent separate bones in some ancestor. By this interpretation the rostral represents four bones, the nasals each three, the frontals each four, whilst the circumorbital bones represent an indeterminate number. It is exceedingly doubtful whether anyone will accept such an interpretation, yet it is the only logical inference from such a reference.

Now turning to Watson's attitude. The vast majority of embryological investigations bearing on the subject at all reveal that in vertebrates, membrane bones are, in all but exceptional instances, developed from one continuous aggregation of osteogenetic tissues, and further than this, that in a great number of instances where the future bones are to make sutural contact, their stromata are originally continuous (Vide Kesteven, 1942, p. 224).

Although the great weight of embryological evidence lies in favour of the attitude of Watson, it does not dispose of the possibility that fusions have taken place. The exceptional instances of fusions are probably *definite* evidence that they have, but there is another interpretation. It is as follows: *A priori* all will agree it is probable that dermal covering bones have been evolved by the coalescence of dermal ossicles and the submergence of their fused bony bases; in which case, it must be agreed that all these bones have resulted from the fusion of very many small centres of ossification, and it may be that the sutures between the individual bones indicate original fracture lines imposed by mechanical strains and stresses, as suggested by Gregory (1915). If this be so, then the number of centres of ossification of lateral-line organ bearing bones in the fishes is without any significance relative to the number of bones incorporated into each of them.

Säve-Söderbergh concludes his polemics (1935, p. 202): "Thus, the study of the Stegocephalians from Greenland has caused not only a thorough revision of the morphology and classification of the Labyrinthodonts, but also a revision of larger groups, resulting in a totally changed classification of the Gnathostome Vertebrates."

Unfortunately, all our attempts at unravelling the tangled problem of the evolution of the Vertebrata are unavoidably compounded from facts *and* our personal interpretation of them. The personal factor cannot be excluded, the evidence is incomplete, and the problem may not be stated as a mathematical formula. None of us, therefore, is entitled to use expressions which convey the impression that the theory advanced is a proven one.

THE INTERPRETATION OF THE CROSSOPTERYGIAN NEUROCRANIUM

Säve-Söderbergh (1936) and Romer (1937) have both attempted to interpret the neurocranium in detail. Exception must be taken to both these efforts because neither writer compared his fossil with the fishes. Without any doubt whatever, both these neurocrania were those of fish, nor do they depart from the general shape and proportions of those of recent fishes. The only marked difference is the break between the anterior and posterior parts. The truth of this statement is brought out by the comparison of the four neurocrania illustrated (Fig. 4). The most striking features on the side wall of the occipito-otic mass in all four are the outer wall of the trigemino-facialis chamber, and the two foramina related to it. These are the most constant and characteristic features in the fish cranium, and the association of the hyomandibular branch of the facial nerve with the hinder of the two foramina and the maxillary and mandibular branches of the fifth nerve with the anterior are just as constant as the bony features. If these features and this constancy of nerve relation are

not the result of direct inheritance from the common ancestral group of fishes, how comes it that not only all the modern fishes but all the surviving ganoids exhibit them? If it is an inherited feature then surely it is present in both *Rhizodopsis* and *Megalichthys*. It is submitted that the features *are* present in both these neurocrania and that they should have been recognised.

In all the recent fishes the basisphenoidal region of the skull terminates just in front of the trigenino-facialis chamber, and the pituitary body lies at, or very close to, the anterior boundary of the chamber.

Both Säve-Söderbergh and Romer identify an outstanding process of the ethmo-sphenoidal mass as a basipterygoid process. The basipterygoid is a process of the basisphenoid bone. This is a basicranial element which, throughout the whole of the vertebrates sutures with the basioccipital bone. These writers follow Watson (1925) in their identification of the basipterygoid process, but, even so, it is doubtful whether the consequential interpretations were recognised by them. If the basipterygoid process was located on the ethmosphenoidal mass then the basioccipital was hinged, not sutured, to the posterior edge of the basisphenoid, and it extended as far in front of the trigemino-facialis chamber as it did behind it. This is a condition which is absolutely without parallel anywhere else in the vertebrate series. There is neither animal nor fish known, in which the basioccipital extends forward beyond the foramina of exit of all the branches of the fifth and seventh nerves.

As a matter of fact, the ethmosphenoidal masses of these two neurocrania are capable of interpretation as perfectly normal fish specimens, absolutely comparable with those of recent forms. The "basipterygoid process" compares very closely with the postero-lateral corner of the ethmoid in recent fishes, and the cavitation in that of *Megalichthys* is very similar to that in the neurocranium of *Paradicichthys* (vide Fig. 2).

The attempt will not be made here, but it is believed that if these two neurocrania were carefully compared with those of the surviving ganoids and modern fishes it would be found possible to interpret all their main features in harmony with those of fishes generally.

Romer, at least, was aware of some of the implications of his interpretation. At the bottom of page 46 and top of page 47 he details the changed proportions in antero-posterior distribution of the various regions and foramina in his specimen.

Romer says of *Megalichthys* that it "may be taken as typical member" of the rhipidistian crossopterygians (p. 44), and there is no reason to doubt the correctness of this statement.

It now becomes necessary again to stress the essential and fundamental similarity of the fossil crossopterygian neurocrania to those of the recent crossopterygians, *Latimeria* and *Polypterus*, and also to those of *Amia* and the modern fishes generally.

It follows that if we accept the interpretation given by the palaeontologists of the crossopterygian neurocrania as correct, then we must try to visualise a re-arrangement of the brain and nerves in all these others to bring about that disposition of these structures which we know to be common to every one of them; crossopterygian and

moderns alike, and all this without any change in the general shape and/or proportions of the neurocrania. We have further to suppose that the basisphenoid bone has migrated back along the base of the skull till it reached the position it occupies in all these others, and without any change in other bones or cranial proportions.

For the writer, at least, this is too difficult an exercise in imagination.

There is another possible explanation, *viz.*, that the whole of the recent fishes were derived from the Actinistia, which would be deemed to have differed fundamentally from the Rhipidistia. There is no evidence in support of such an explanation; it would be merely an assumption, necessitated by acceptance of the interpretation of the rhipidistian neurocrania.

"On the Coelacanth Fish." D. M. S. Watson (1921).

Doubtless Watson's descriptions and illustrations of the fossils present the characters and contours of their component parts correctly. This being granted, his identifications of some of the bones, and the interpretations he gives to their features, are incomprehensible to the student of the crania of modern fishes.

That which he identifies as the basisphenoid is a bone which satisfies all the criteria of a presphenoid ossification; such, for instance, as that of *Amia* (Fig. 4c).

The bone which it has been agreed upon to designate basisphenoid throughout the fishes, other than in this coelacanth *Macropoma,* is placed entirely in the floor of the neurocranium in front of the pituitary fossa. If in an attempt to identify this "basisphenoid" bone in *Macropoma,* one disregards the fishes and turns to the lower tetrapods, one would still be at a loss to find a basisphenoid bone which, like this, belied its name as a basal bone and extended to the roof of the cranium.

The absence of ossification in the "lower part of the basisphenoid" (p. 322) increases the similarity of this bone to the sphenoid ossification of *Polypterus.*

A comparison of Watson's figures 1 and 2 leads to the belief that he has failed to recognise a fracture of the base of the cranium immediately behind this sphenoid ossification. Behind the fracture, it is now suggested, the posterior portion of the parasphenoid with a normal ascending flange has been displaced upwards, and this bone, which Watson identifies as the prootic, is really the posterior moiety of an expanded parasphenoid, which, as in *Polypterus,* covered an entirely cartilaginous portion of the otocrane.

That the inner surface of an extensive "prootic" should be a plane surface devoid of otic recesses is hard to believe. The prootic is a bone developed endochondrally in the anterior portion of the capsule. On the other hand a plane internal surface would be natural to, and quite in conformity with, the mode of development of an ascending expanded posterior portion of the parasphenoid bone.

Stensiö was perhaps correct in his belief that this "prootic" included an opisthotic element. It is probable that better material will disclose a suture interrupting the continuity with the posterior of the two superior wings of the bone.

The skull of *Macropoma* as interpreted by Watson is completely anomalous, but if we visualise the so-called prootic moved down and just a little backward, leaving a gap filled by cartilage in the fresh skull between it and the sphenoid ossification, and then fill in a suture across the lower end of the posterior superior wing, the skull becomes essentially similar to that of *Polypterus*.

Watson's identifications of the components of the palate are subject to the grave suspicion that he has been unduly biassed by a desire
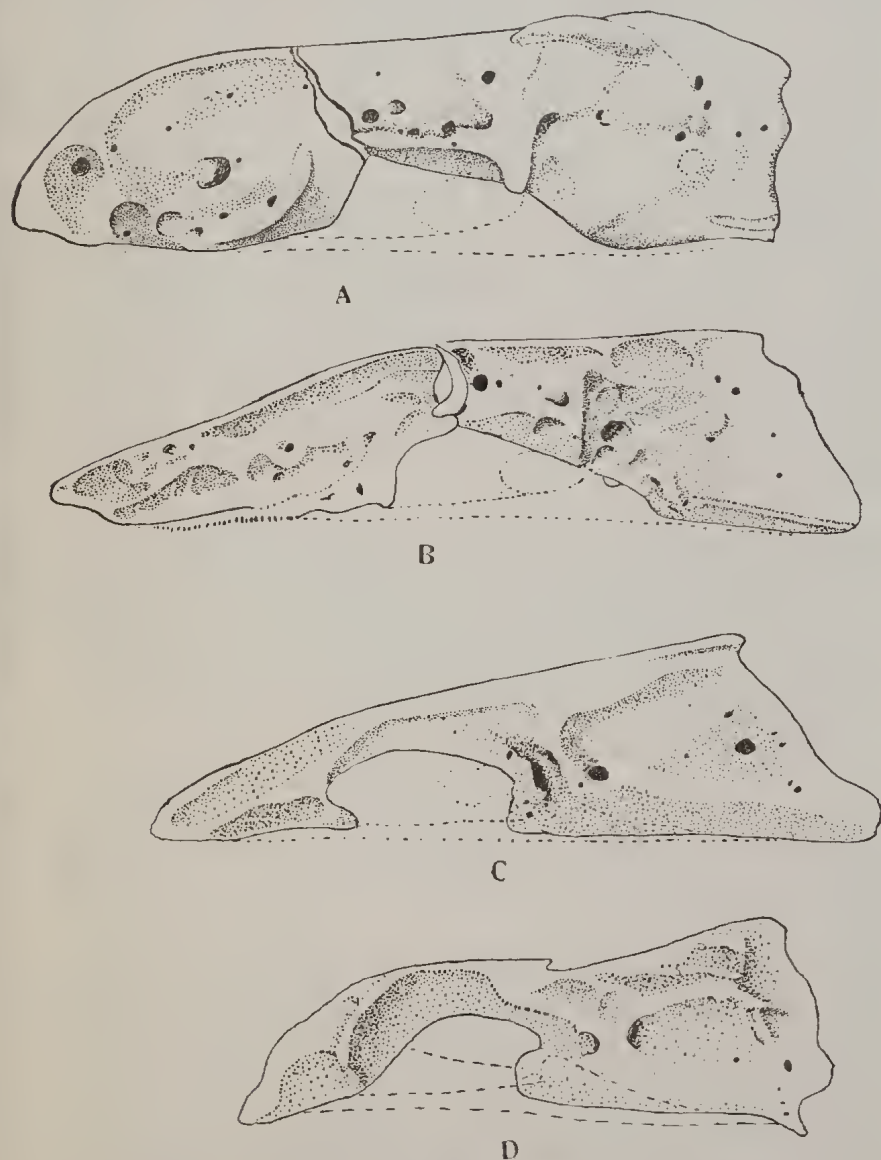
A

B

C

D

Fig. 4.—Crania of R. Rhizodopsis (from Säve-Söderbergh), B. Megalichthys (from Romer), C. Amia (from Allia), and D. Epinephalus. The actual or probable situation of the parasphenoid bone, and intorbital septum has been indicated in dotted lines.

to find resemblance rather to the lower tetrapods than to the fishes. No attempt was made to interpret the observed features by comparison with known fish crania.

He tells us that the bone which has been previously identified as a "hyomandibular" by most authors "has been" correctly determined by Stensiö as a "metapterygoid." In the explanation of his figure 5 he introduces confusion by equating the metapterygoid with the epipterygoid. It is hardly necessary to point out that the metapterygoid bone of the fishes is not part of the quadrate and, therefore, cannot, by any stretch of the imagination, be regarded as homologous with the epipterygoid bone of the reptiles.

If Watson's description of the coelacanth palate and palato-quadrate be correct, it follows that the whole structure was attached to the skull only by "tough membrane" between the mesial margin of the pterygoid and the parasphenoid. This is hard to believe.

When it is remembered that hyoid suspension of the quadrate characterises every known fish, it is exceedingly difficult to accept the interpretation offered. The assumption that the hyomandibular is absent presents itself as entirely gratuitous, and depends on nothing but a failure to find. A much more reasonable explanation of its absence would have been to assume that so much of it was cartilaginous that any bony portions which may have been present had been displaced by the rotting of the cartilaginous portion. Since the work was written (in 1921) Smith's description of the living Coelacanth *Latimeria* has appeared. The hyomandibular of this fish is largely cartilaginous.

The following passage calls for criticism:—"The metapterygoid, certainly an ossification on the palato-quadrate cartilage . . . agrees closely with one of the continuous series of ossifications which occurs in cartilage in Osteolepids and rather strikingly with the epipterygoid (!) of an Embolomerous Labyrinthodont which I am describing shortly. There can be no doubt that the bay in its upper edge transmitted the maxillary and mandibular divisions of the fifth nerve, and that the ophthalmicus profundus passed out in front of it" (p. 333).

If this passage had been worked as below, it would not have been open to the objection that expressions of opinion are given as statements of fact — "The metapterygoid, probably an ossification on the palato-quadrate cartilage . . . agrees, etc., . . . *It is believed* that the bay on its upper edge transmitted the maxillary and mandibular divisions of the fifth nerve and that the ophthalmicus profundus passed out in front of it."

In its original form the whole passage is unacceptable. If Watson had stated that *he* was certain and that there was no doubt in *his* mind, that would have been all his material justified him saying. Even as a statement of opinion the passage would be open to criticism.

In view of the fact that these branches of the fifth nerve very rarely impress their course on bones of the suspensorium or palate in living fishes, either teleost or ganoid, and that they all issue well in front of the articulation of the suspensorium with the skull, the course postulated by Watson is absolutely without foundation on fact or analogy. One is forced to the conclusion that the only reason for giving such an interpretation to the "bay on its upper edge" was the

author's desire to increase a fancied resemblance of this fish "meta-pterygoid" to the "epipterygoid" of the embolomerous amphibians*.

Watson returns to the presumed absence of the hyomandibular on page 336, where we find the following:—"As Stensiö has pointed out, we have in coelacanths a complete loss of the hyomandibular as a supporting element of the jaw. This loss is an *exact parallel* to that which has occurred in Tetrapods and Dipnoi." (The italics are mine).

This last statement is very far from true. Edgeworth demonstrated quite definitely that the hyomandibula is developed in *Ceratodus*. Even if we regard the vestigeal hyomandibula of *Ceratodus* as being without significance in the present connection, there is still no parallel at all between the conditions found in the Coelacanths and the Tetrapods and Dipnoi.

In the former the quadrate is separated from the skull by a hyomandibula bone and a metapterygoid, which latter is so like the metapterygoid of *Amia* and *Polypterus* that there is little doubt that it is the same bone. This cannot, by any stretch of the imagination, be homologised with the epipterygoid. The epipterygoid of tetrapods is undoubtedly the homologue of the processus ascendens quadrati, and is developed endochondrally, that is to say, it is a true cartilage replacement bone; the metapterygoid of the fish is developed ectochondrally and extended beyond the cartilage as a membrane bone and is not a part or process of the quadrate. The long gap between the quadrate and the skull was in all probability filled, in the living coelacanth fish, by a cartilaginous or largely cartilaginous hyomandibula (page 106).

In the tetrapods the hyomandibula has been reduced to the stapes and the quadrate is attached to, or articulates with, the skull. Its final evanescence has been demonstrated by Edgeworth in *Ceratodus*.

Clearly there is no parallel here.

A. "The Structure of Certain Palaeoniscids and the relationships of that Group with other Bony Fish," D. M. S. Watson (1925).

B. "On Some Points in the Structure of Palaeoniscid and Allied Fish," D. M. S. Watson (1928).

The critical reading of these two communications gives rise to two general impressions, firstly, that the writer has brought to the work a familiarity with the cranial osteology of the mesozoic fossil amphibians; and that, in the absence of counterbalancing knowledge of the cranial structure of the Teleostei and Ganoids, the whole of the work has been unduly influenced by the knowledge he had. Secondly, one feels that the writer has served but a short apprenticeship with the scalpel and the dissecting tweezers, for he displays a peculiar courage in his identification of the various foramina and grooves which he finds in his fragmentary fossils. Such courage could hardly be possessed by one familiar with the difficulties of dissection and the unreliability of features in the modern forms of the same character as those he relies upon.

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* If these latter had already cast the ascending process loose to constitute an independent epipterygoid, it is hard to understand why no recent amphibians exhibit such a feature.

In the result, his reconstructions of the coelacanths are interpreted to harmonise, not with fishes generally, but with the embolomerous amphibians, and with other poorly-known fossil fish.

In the following brief review it is assumed that his statements of *fact* are truly recorded, and depicted with approximate correctness in the illustrations. On these assumptions an attempt will be made to compare the structures with completely known fish. This attempt is made because it appears desirable to demonstrate that, when viewed in the light of complete familiarity with forms whose osteology is perfectly understood, all the features hitherto recorded of the known fossil fish are capable of being more or less perfectly harmonised with those of the modern forms.

Experience teaches that when, having dissected and determined the soft structures related to the foramina and grooves which a particular skull betrays, one takes in hand another with *similar* osteological features (be it noted not with *approximately* or *nearly* similar), one feels entitled to interpret all its features in terms of the dissection already carried out. Experience also teaches that even with this conservative procedure, we are liable to make mistakes. When, on the other hand, the disposition of the bones and the foramina are different from those of our dissected example, we do not feel entitled to guess at the interpretation of the foramina. Only after careful dissection, usually of more than a single specimen, does the careful anatomist feel confident in discussing the relation of soft structures to the bones. Thus, the most careful dissection of the Percoid skull and the most perfect familiarity with its features and the relation of the bones to the soft structures would not enable one to describe the relation of the nerves and blood vessels to the skulls of *Polypterus, Amia, Accipenser,* any Selachian, an Eel (*Anguilla*), or a Cat Fish (*Gnidoglanis*), nor would the dissection of all but one of these enable one to interpret the foramina in the last with confidence. Again, the dissection of one Plagiostome, or, indeed, of many, would not enable one to state definitely the relationship of nerves and blood vessels to the cartilaginous cranium of a type not previously dissected.

It is, therefore, clearly a dangerous proceeding, and one likely to lead to very erroneous conclusions, for any palaeontologist, except in very exceptional instances, to write of any foramen that it "clearly transmitted" this or that nerve or vessel, or that "it could have transmitted none other" than this or that.

At the moment I can recall no instance among living fishes in which the emergent branches of the fifth and seventh nerves are not closely associated both on the inner and on the external surfaces of the skull, nor can I recall an instance where these nerve trunks do not, except the ophthalmicus superficialis and hyomandibular branches of the facial, emerge close to the cranial floor in the anterior part of the prootic region.

Almost invariably they leave the cranium either through the prootic bone or through a notch in its anterior margin; at times, all together through one single large common foramen, at others, through several small foramina closely gathered together. When more than one foramen is present, one can tell only by dissection which trunk or ramus

occupied which foramen, for there is no constancy in their relation one to another.

There are several instances of the dangerous practice referred to throughout the two works under review; one instance only need be quoted, namely, the description of the "facialis chamber" in "Palaeoniscid B" which is epitomised, as it were, in Figure 19 on page 843 of the earlier paper. I have to confess that after years of study of the fish's skull, and after dissecting a reasonably representative series of the heads, I should be absolutely at a loss, on being presented with one so strange as this palaeoniscid, to interpret all the foramina. Dr. Watson does this with confidence, and even goes so far as to imply that the hyomandibular trunk of the facialis divides into two before emerging from the skull; or are we to understand that he finds in these foramina evidence that this fish had an extra mandibular branch of the facialis? The identification of the foramen for the patheticus in the bones of a fossil excites one's admiration, and at the same time it awakens one's suspicion. I have in very rare instances been able to find this foramen after carefully dissecting out the nerve. Its position is far from constant in the living fishes.

It is noticeable throughout Dr. Watson's work that he constantly identifies facialis and trigeminal foramina separated from one another. Having in mind the fundamental teleostoman characters of the fossils he is dealing with, one cannot but wonder whence comes the evidence on which this identification is based, and one feels that the practice results from the "tetrapod" frame of mind.

Turning now to the covering bones of the skull and dealing first of all with the dorsal aspect of *Chirolepis trailli*. As restored by Watson, there is nothing in this skull to separate it from the modern teleostean type. True, one cannot point to any one skull amongst the moderns which exactly resembles it; on the other hand, a similar remark would apply to any one of the modern generic types; there are, outside the genus, no skulls whose dorsal pattern is precisely the same.

The dorsal pattern of *Chirolepis* is essentially similar to that of *Dactylopterus* (E, Fig. 1), but the latter has developed a supraoccipital between the parietals which is not present in the former. However, this feature cannot be regarded as of phylogenetic importance, for the allied scorpenid *Peristedion* has the supra-occipital covered by the parietals just as the fossil has. The presence of the occipital transverse limb of the lateral line canal system enables one to identify the post-occipital scutes in the two forms, whilst the post-temporal is similarly identified by the presence of the homologous canal in both.

In thus identifying the bones by their contained lateral line canals, I follow a well-established practice. To quote Watson himself (1925, p. 820), "the passage of the main canal through the supraoccipital and intertemporal shows that these bones are homologous with the corresponding elements in the Osteolepids, or, at any rate, belong to the same row . . ." This quotation is particularly apt because it applies to the same bones in the scorpenid. In front of the post-occipital the canal passes across two bones before reaching the frontal, just as in the palaeoniscid. These, by Watson's own criteria, will be homologous elements in the two forms.

The moulds of the neural crania of two Palaeoniscids which Watson depicts on page 834 and which he describes, present no features wherein they differ fundamentally from those of modern bony fishes. The outer wall of the so-called spiracular canal is in all probability really only the outer wall of the trigemino-facialis chamber. This is a very constant structure in the prootic region of the modern fish skulls, and, as in the palaeoniscid skulls, lies just below and in front of the hyomandibular articular facet. Its upper aperture probably transmitted the same nerves and vessels as in the modern forms, that is to say, the vena capitis lateralis, and the orbital artery passed to and fro through it whilst the hyomandibular branch of the facialis issued from its postero-superior opening, and the remainder of the trigemino-facialis trunks, except the palatine branch of the facial, issued antero-inferiorly.

It is unfortunate that Watson should have used such definite language in his description, for the whole of his interpretations and statements relative to the soft structures are entirely conjectural. On page 842 he declares quite confidently, and without any reservation, absolutely as though they were statements of fact, that various foramina transmitted various nerves and vessels. It is here that occurs the confusion relative to the branches of the facialis. He describes the hyomandibular branch as issuing through one foramen, and a mandibular as issuing with the palatine through another.

A more astonishing example of this independent uncontrolled identification is to be found on page 52 of the later of these two papers.

"Ventrally the outer margins of this bony plate (the 'Basisphenoid') are produced into long basipterygoid processes, which bear a depressed area for articulation with the palato-quadrate on the upper and anterior faces. The root of each basipterygoid process is perforated by a foramen which leads into a canal running upward and outward in the basisphenoid until it leads into a groove on the upper surfaces of the processus ascendens of the parasphenoid."

"From this canal a branch passes downward and inward to perforate the parasphenoid and open on the ventral surface of the skull. The main canal *must** have transmitted the palatine branch of the facial nerve, the branch being for a ramus pretrematicus, passing to the skin of the mouth, as Herrick has described in *Menidia*." (*Italics are mine.)

For comparison with this statement I quote Herrick (1899, p. 173) on *Menidia*: "A large bundle of communis fibres runs from the ventral surface of the geniculate ganglion, enters the same foramen as the truncus hyomandibularis, crosses the latter nerve and gives to it a considerable communis component, as already described. Immediately *after its emergence from the cranium* it divides into two approximately equal portions; one, the ramus palatinus, passes cephalad *along* (not *in*) the cranial wall under the origin of the m. adductor arcus palatini, the other, to which I have applied the name of ramus pretrematicus VII, turns directly ventrad along the caudal and inner face of that muscle and between it and the large pseudobranch, . . . " again not in a canal.

It is clear from this description that in no part of its length is the ramus palatinus facialis in *Menidia* enclosed in a bony canal, nor is the tiny ramus pretrematicus.

Herrick's description would lead one to infer that the canals described by Watson did *not* enclose the nerves.

The reference to *Menidia* is peculiar, because a comparison with *Amia* would have provided some resemblance. In this form the palatine nerve lies between the parasphenoid bone and the sphenoidal cartilage, and a similar position for the nerve in *Lepidosteus* has been described by Norris (1925, p. 371).

The parallel is, however, far from exact. In these forms the canal between bone and cartilage is reached by the nerve from without, and its posterior end is apparently much further forward than is the posterior end of the canal in Watson's drawing of *Cosmoptychius*. No part of the canal for the palatine branch of the facialis in the two holostean forms lies in the basisphenoid region. In both cases the palatine nerve is accompanied by components of the glossopharyngeal nerve and by blood vessels.

Actually the most that can be said of the canal in question is that it is *possible* that it transmitted branches of the glossopharyngeal and facial nerves and more possibly blood vessels, but as to the source of the latter one would hardly be justified in hazarding a guess.

On page 848 of the earlier of the two papers Watson seriously discusses the form of the brain in an Osteolepid and in the Palaeoniscids, basing his whole discussion on internal casts of the neural crania. He says, "the cerebral hemispheres of *Osteolepis*, *if* we may judge from the character of the chamber in which they lay, were long and of considerable size. *In fact*, the brain, as a whole, *cannot* have differed very greatly from that of Ceratodus and an Amphibian."

Towards the end of the next paragraph we meet the following, relative to the brain of the Palaeoniscids: "It is probable that the *reduced cerebral hemispheres* imply that the sense of smell was no longer, as it is in all primitive fish, the chief agent in the recognition of food, and that the extravert type of cerebral hemisphere had already been introduced in them."

Like much else of the work, this is simply speculation, quite unsupported by factual evidence, and based on purely personal interpretation of the structures observed. In the same category is the statement on page 845 of the same work that "The seventh nerve arises by a single root, so far as can be seen from the skull, ..." One only wonders that our author does not tell us the relations of the nucleus of the facial nerve to that of the trigeminus!

Watson (1915, p. 848) says that in *Osteolepis* the outer wall of each olfactory capsule is perforated by a small circular external nostril, "its ventral surface by a triangular internal nostril, ..."

This again is entirely a question of interpretation, and not a statement of fact. (See postea p. 118).

Having in mind the licence which Watson has allowed himself in the interpretation of neurocranial structures, one cannot but view with suspicion his interpretations of the various fragmentary palates he attempts to restore.

At the outset one may point out that the identification of a notch at the anterior end of the palatal complex of *Nematoptychius* (fig. 26, p. 858) as being for the transmission of the mandibular and maxillary branches of the Vth nerve is obviously incorrect, at least in so far as concerns the mandibular ramus. The mandibular ramus must have passed down behind the gape of the mouth and close to the lower jaw joint. There is no reason to suppose that it took a course, entirely without parallel, far forward and then turned back.

Watson's figures 22, 23, and 24, represent palates which are subject to interpretation in terms of those of *Lepidosteus* and *Amia*. Although much fragmented, it appears unquestionable that that of *Eleonichthys aitkini* is the least distorted, and presents the bones in the nearest approach to their natural position. In the others, if Watson be correct in assigning them all to the same genus, the bones must be thrust from the midline and laterally compressed, or else the thin inner area of the palates has been lost. This appears to be supported by the condition present in the allied *Euryonotus crenatus* (1928, fig. 12, p. 62) and by the contours of both the palaeoniscid neural crania figured and described by Watson. These indicate that a relatively narrow interval was present between the hyomandibular articular facets on each side of skull.

A comparison of Watson's figure 23 (1925, p. 855) of the palate of *Eleonichthys aitkini* with the palate of the short-headed *Lepidosteus* leads to the belief, assuming that the illustration correctly depicts the fossil, that these two fishes are very similar. *E. aitkini* apparently possessed a true basipterygoid process articulating with one of the medial palatal bones. Since the process appears to have been in the same situation as that of *Lepidosteus* it is certainly not unreasonable to believe that it articulated with the homologous palatal element, that is to say, with the metapterygoid, and there appears to have been the same relatively extensive gap between the articulating bones and the hyomandibular behind in both forms. Apparently the whole palatal complex and its posterior mandibular suspensory components stood down well below the plane of the basis cranii, and, in the specimen illustrated, it has been displaced laterad and caudad. The bone which Watson identifies as the pterygoid is the mesopterygoid of *Lepidosteus*. In the fossil fish it is more extensive than in the other and recalls that of *Polypterus*. The bones which Watson identifies as Palatines I, II, and III, and ectopterygoid, are certainly identifiable as an extensive, fragmented, palatine in front, and ectopterygoid behind. The little fragments identified as suprapterygoids IV and V are in all probability the fragmented metapterygoid. The unidentified fragment lying behind the ectopterygoid is conceivably portion of the quadrate.

This interpretation of the palate of *Eleonichthys* is not offered as a definite identification of its elements but as an indication that, on the evidence before us, it is possible to interpret it in harmony with already completely known fish palates, and because it is undesirable whilst such an interpretation is possible to create new palatal types on such fragmentary evidence as these crushed and distorted palates provide.

One cannot conclude this review of these two papers without commenting on Watson's identification of the basipterygoid process in several of the fishes described.

The basipterygoid process is an ossification of the para- or immediately pre-pituitary region of the cartilaginous basis cranii, and is a process of the basisphenoid bone.

Nowhere among the living fishes do we find a basipterygoid process which conforms completely to the above definition. In *Lepidosteus*, however, there is an ossification of the correct region of the basis cranii, but the ossification is by an extension forward of the prootic bone, not the basisphenoid.

Kesteven (1926, p. 121) suggested that we should regard as completely homologous, bones which ossify in precisely similar regions of the primary chondrocranium, even though they may not develop from similar centres of ossification, proposing at that time to designate those which develop from the usual centre of ossification, "determinate"; and those which develop by extension from the centre of ossification of a contiguous bone, "predeterminate."

Applying this principle in the present instance we may accept the identification of the basipterygoid process in *Lepidosteus*. It is truly a basipterygoid process, but is a predeterminate form thereof.

Comparison of *Lepidosteus* with Watson's illustration of the fragmented palate of *Eleonichthys aitkini* leads one to accept without reservation the identification of a basipterygoid process immediately medial to the little palatal fragment labelled S.Pt.IV. It is also very probable that the parasphenoid extended much further back than Watson's interpretation allows.

In the case of *E. binneyi*, however, it is clear that the tubercle which is identified as the basipterygoid is placed a long way too far forward to be that structure; there can be little doubt that this tubercle is actually antorbital in situation.

In *Polypterus* and quite a number of the Teleostei there is a projection of the parasphenoid below the basis cranii in the region in which the basipterygoid process is found. This is a fundamentally different structure to the true basipterygoid process. It is not developed endochondrally from the primordial basis cranii.

It is to be observed that in *Lepidosteus*, in which the true process is developed, there is related to its underside a spur of the parasphenoid. In *Polypterus* and the other examples mentioned there is no cartilaginous or endochondral bony process related to the parasphenoid spur.

In *Cosmoptychius striatus* (1928, p. 52) the basipterygoid process is correctly identified by Watson as a process of the basisphenoid (Watson, 1926).

Watson asserts that *Dipterus valenciennesi* presents so many features which resembled those of the contemporary Osteolepids that the two groups (Dipnoi and Osteolepida) "arose from a common ancestor not much earlier in date," and he continues, "it is from this hypothetical fish that I believe the Amphibia to have risen. The evidence on which this view is founded is most convincingly presented by a comparison of the structures of the skeleton, of the body form, and movements, and of the mode of life, in an Osteolepid

and an Embolomerous amphibian. In order to secure the materials
for such a comparison I have been forced to investigate the osteo-
lepid structure anew . . . ." (p. 195).

Dr. Watson is certainly ingenuous; he does not hesitate to admit
that he was already convinced before studying them that, if the
fossil fish were studied, evidence in support of his preconceived
theory of the evolution of the Amphibia would be found in their
structure.

It was apparently this mental attitude which prompted the follow-
ing paragraph. "The exoccipitals in the Osteolepida reach up to a
well-developed supraoccipital, which in *Osteolepis stretches forward
over the whole of the hind brain,* as it does in the Embolomeri. The
otic capsule forms a paroccipital process which supports the tabula,
and may or may not be in contact with the skull roof for the whole
of its length, precisely as in the Amphibia. As in them, the anterior
part of the brain lies in a cavity in the upper part of a thick inter-
orbital septum whose lower edge is the parasphenoid." Watson per-
sistently makes the error of designating the parotic process "paroc-
cipital." The paroccipital process lies ventrally to the otic capsule,
the parotic lies dorsolaterally to it.

"The basisphenoid in both fish and Amphibia has definite basi-
pterygoid processes with which the epipterygoids articulate."

As was the case in the last papers reviewed, much of the apparent
statement of fact in these two paragraphs is largely interpretation.
In the previous paragraph to that quoted, it is stated that the osteo-
lepid brain case *"is not divided into separate bones in any known speci-
mens."* Yet we are told that this osteolepid brain case resembles the
Embolomeri *because its component bones occupy certain areas.*

Examination of his illustrations discovers that the parotic process
of the Embolomeri is infinitely better developed than that of the
osteolepids, in which it is essentially similar to that of almost any
typical acanthopterygian percoid skull. In these forms it has not
been dignified by separate designation or definition. In the Embolo-
meri, if they be all similar to that of *Orthosaurus pachycephalus,* the
parotic processes are extensive and recall those of certain of the
reptiles and modern amphibians.

The statement relative to the situation of the anterior part of the
brain is absolutely without any foundation in fact; on the contrary,
remembering that these were fossil fishes, such evidence as may be
obtained by the examination of the cranial cavities of the modern
ganoids and teleosts, and consideration of their casts relative to the
form and situation of the contained brains, suggests that the fore-
brain did not extend appreciably past the well-defined temporal fossa
of perfectly typical teleost outline which Watson depicted in the
Palaeoniscid in figure 20 of the 1925 paper, nor much anterior to the
typical trigemino-facialis chamber illustrated in the top drawing of
figure 78 of the communication under review.

Not only is this so, but his own descriptions and illustrations belie
his homologies. It should surely have been obvious that the structures
which he labels basipterygoid processes in the two reconstructions of
fish crania illustrated in his fig. 4 could not be regarded as basiptery-
goid processes.

In the *Baphetes*, on the other hand, there is obviously a typical basipterygoid process of the basisphenoid essentially, one might almost say precisely, similar to that of many reptiles. In the *Eusthenopteron* a critical examination of Bryant's description and illustration of the orbitosphenoid must surely satisfy one that it is the posterolateral corner of a relatively normal ethmosphenoidal ossification which is here identified as a basipterygoid process.

One must also take exception to Watson's assumption that the metapterygoid of the Osteolepida is the homologue of the epiptery-goid of the Embolomeri (vide postea, pp. 119-121).

This assumed homology rests only on his further assumption that certain branches of the fifth nerve passed in certain relation to the dorsal margin of the bone. Even if we grant his assumption, as to the spatial relations of the bone and the branches of the nerve, the homology is by no means proven. Kesteven demonstrated quite con-clusively that the relation of the branches of the fifth nerve to homo-logous bones is variable, and unreliable as a definitive feature in deter-mining homologies (Kesteven, 1926).

As a matter of fact, this homology is so far fetched that it could only have been suggested by one in search of evidence in support of a preconceived theory; it would be amusing if it were not regrettable.

Ridewood, in 1904, described the neural crania of a number of more or less abnormal teleostean forms, and several of his illustrations have been reproduced by Gregory (1933), who gives in addition illustrations of a number and a wide range of normal crania. It is suggested that if Watson's illustrations of the neural cranium of *Osteolepis* and Bryant's *Eusthenopteron* be compared with these and with figure 4 of this communication, such a comparison must con-vince the unbiassed student that the fossil neurocrania are readily interpretable in terms of that of the modern fishes. The resemblance is essentially to the fishes. One notes that the parasphenoid is missing.

Watson writes (p. 234), "The neural cranium of the osteolepids was first, though quite inadequately, described by Rohon; later again misleadingly, by myself and H. Day and by E. A. Anderson; and finally more successfully by W. L. Bryant. Dr. Bryant's description is, as Dr. Stensiö informs me, and I have been able to confirm, from an examination of the original material, inaccurate in certain respects . . . ."

Notwithstanding all this difficulty and divergence of interpreta-tion, Dr. Watson uses his latest interpretation with complete confi-dence to supply evidence as to the evolution of the Amphibia. He tells us that the arguments of his communication rest upon the structures of the Embolomerous Amphibia and of the Osteolepid fish. As a matter of actual fact, then, the whole of his argument on their cranial structure in support of the crossopterygian origin of the Amphibia, rests largely on assumed structures which may or may not have been present in the neurocrania of *Osteolepis* and *Eusthenopteron*, and on the similarity of the dermal covering of the skulls.

Dr. Watson's three drawings of the lateral view of the neural crania are misleading, and almost partake of the nature of "special

pleading." His other illustrations show very plainly that these neural crania in a dorsal or ventral view would have shown even less resemblance than do these lateral views.

The similarity of the dorsal dermal pattern of *Cheirolepis* to that of modern Acanthopterygii has been discussed previously. Gregory (1933) has reproduced Watson's illustration of this and of the three illustrated on page 197 of the work. These may be conveniently compared with the dorsal pattern of the moderns illustrated on the later pages of Gregory's work.

At the same time it may be pointed out that if similarity of dorsal dermal pattern may be accepted as evidence of genetic relationship, then the converse should be true.

A classification of the modern fishes based on such a premise would indeed lead to a chaotic grouping of the living forms.

Watson writes (p. 245), "A comparison with *Macropoma* (one of the Coelacanth fish) shows quite clearly that the pituitary fossa lay within the basisphenoid between the basipterygoid processes, and the position of the pineal foramen confirms the view that the thalamencephalon lay in the hinder parts of the anterior section of the neural cranium." There is no certainty that a pineal foramen is present. Many modern fishes exhibit deficiencies in the dorsal roof, in the position of a possible pineal foramen, but these are not of that character.

Quite apart from the fact that the basisphenoid bone of *Macropoma* differs markedly from that of the *Osteolepida*, as restored by Watson (and there is no certainty that the bone in *Macropoma* is a basisphenoid at all), Watson has himself advanced the strongest evidence against the possibility of the brain extending into the "anterior section of the neural cranium."

He has advanced evidence that there is a joint between the two "sections" of the "neural cranium," and that the joint functioned as such, that is to say, he believes that there was actual movement about this joint.

It appears highly improbable that the brain should have been subjected to stress and strain by lying across a joint. There is no doubt that the joint between the dorsal derm bones in the Dinosaur skull (with which Watson compares it) lies entirely in front of the brain, as does that of the parrot's skull.

The Braincase of the Carboniferous Crossopterygian Megalichthys nitidus, by A. S. Romer.

The neurocranium has already been discussed, but further comments are called for. In a later paper (1941) he has described the hyomandibular of this fish in detail. His specimen indicates that the bone was binarticulate and he was of the opinion that this was an unique feature. He states (p. 147), "in all fish hitherto known, the hyomandibular has but a single attachment." This is quite erroneous, the hyomandibular bones of recent fishes present one, two or three distinct and separated articular facets. Kesteven (1926, p. 208) proposed the terms mon-, bin- and trin-articulate as descriptive of both the bone and the type of articulation. It is possible that this hyoman-

dibular was attached to the skull in the same manner as the binarticulate types amongst the recent fish. It has not yet been found actually in place.

It is believed by Romer and others that the two articulations of the bone were placed above one another. Whilst the two depressions present on the side wall of the skull justify the belief, it is possible that the lower really gave attachment to the anterior end of the branchial skeleton, it is certainly in the position of such facets on numbers of the recent fish.

There are quite important factors which give support to this suggestion. First, it seems reasonable to assume that the hyomandibular was, at least, as firmly bound to the opercular bones and cheek plates as in living archaic fishes. Therefore, if the bone was articulated to the skull at two points, one above the other, then all these bones must have been so firmly fixed that the movements of respiration would have been impossible.

Neither abduction, adduction nor rotation would have been possible about the hyomandibulo-cranial joint, but on the other hand, the well-developed articular heads of the bone indicate a functional joint. If Romer's illustration of the hyomandibular bone is correct, then, with the two facets in place in the depressions he illustrates on the skull, the shaft of the bone would have, apparently, been directed upwards and backwards. If, as in other binarticulate bones, the two joints were placed at the same level, one behind the other, the direction of the bone would have been normal, and, of course, the normal movements of respiration could have taken place.

Romer writes that comparison with *Ceratodus* suggests that "two small tubers" on the ventro-lateral surface of the otic capsule "afford origin for branchial levator muscles."

The facts are that in *Ceratodus* the levator branchii muscles arise from the underside of the cartilaginous roof of the branchial fossa and from the perfectly smooth surface of that ceiling (Kesteven, 1944, pp. 140-141). It is very exceptional for muscles to arise from tubercles or tuberosities on the skull of any of the fishes. The characteristic condition is that they arise from flat surfaces, and from fossae separated by flanges or ridges, to which the muscles, commonly, are not attached.

In the present instance it is evident that Romer did not make an examination of the actual conditions in *Ceratodus*. Had he done so his dissection would have prevented him from making such a comparison.

The whole of the arguments of Romer and others in the attempt to establish similarities between the suspensorium of the Crossopterygians and that of the Tetrapods, are discounted by the fact that in the Fishes, suspension is effected by the hyomandibular, which is placed between the quadrate and the skull. The Chimeroids are the only fish in which the quadrate is attached directly to the skull. Romer discusses the attachments of the quadrate to the skull, and the question whether they are primary or secondary. The weight of embryological evidence was accepted, two or three decades ago, as proving them to be secondary, and this has not, I believe, been questioned since. All the evidence in question also indicates that no part of the

hyoid has entered into the formation of the attachment of the quadrate. Therefore, in the presence of a hyomandibular, we are in the presence of a fundamentally important feature which distinguishes the whole of the rest of the fishes from the Chimeroids as well as from the Lung fishes and the rest of the tetrapods.

It should be noted that the whole of the arguments are directed towards establishing similarities and homologies between Crossopterygians and tetrapods which are obviously and admittedly present as between Dipnoans and Tetrapods. Although cognizant of this, palaeontologists have failed to recognise its importance because the palate of the Dipnoans is so peculiarly specialised.

Romer writes, "it is unquestionable that the crossopterygians and lung fishes are allied stocks. But comparison of their endocranial structures is difficult. Part of this is due to marked difference in jaw structure and articulations. But further difficulties are due to the fact that living lung fishes have surely departed widely from the ancestral type in braincase structure, as they are known to have done in the case of the dermal skeleton."

There is no evidence that the braincase of the modern Dipnoans has departed in any important detail from that of the early forms, or from the ancestral type. The modification of the dermal shield cannot be accepted as evidence of any such change.

On the Structure of the Snout of the Crossopterygians and Lower Gnathostomes in General, E. Jarvik (1942).

Jarvik describes the snouts of three crossopterygian species in great detail. The work is based on reconstructions from serially sectioned material, and the correlation of features presented in several specimens. There is every reason to believe that he has presented us with correct descriptions and illustrations of the three snouts.

Jarvik has no doubt that both the rhipidistian species illustrated were choanate, and at first sight his descriptions and illustrations of *Eusthenopteron*, at least, appear convincing. A more critical examination of his evidence, however, leaves one very much in doubt. The specimen is undoubtedly portion of a fish, and the description is confined to bony parts. In all recent ganoids and in a very large number of the modern fishes there is much cartilage related to the ethmosphenoidal ossifications. In the absence of this cartilage the nasal capsules of quite a few forms would appear to open ventrally. Also there is a gap, in the situation of the "internal naris" in the palate of *Eusthenopteron*, between the palatal bones of many recent fish. This gap is made good in the living fish by cartilage and/or connective tissue. It must not be forgotten that the surviving ganoids are not choanate. These recent ganoids are really the only factual evidence we have as to what the structure of the ganoids was.

After the most detailed "restoration" of the constitution and distribution of the cranial nerves and other soft structures in relation to the snouts of *Porolepis* and *Eusthenopteron*, Jarvik concludes that the Urodeles are derived from the Porolepiformes, and the Anura from the Osteolepiformes.

If Jarvik's restorations might be accepted as evidence, there is no doubt that they would support his contention, but remembering that

the neurocrania are undoubtedly those of fish, and present most of the characters of fish neurocrania generally, there is no doubt that any competent anatomist could "restore" the distribution of the cranial nerves and location of the main blood vessels in accord with the general pattern of the fishes just as convincingly, and with, perhaps, more justification. His contribution to factual evidence is his careful description and illustration of the three snouts. All his restorations are merely reiterations of his conviction that they exhibit amphibian characteristics. The evidence supporting his conclusion as to the derivation of the two recent amphibian groups resolves itself into the facts that the nasal capsules of the Porolepiformes are widely separated, whilst those of the Osteolepiformes are separated by only a nasal septum.

Jarvik overlooks, or neglects, the fact that in some of the Urodela the nasal capsules are separated by only a septum as in the majority of the Anura, whilst in some of the latter the capsules are separated as in the majority of the Urodela. These facts throw very grave doubts on the verity of his conclusions.

It might, conceivably, be suggested that since the capsular conditions cited by Jarvik are, in the main, characteristic of each of the two classes, those which depart therefrom are degenerate, or otherwise specialised. As a defence of his thesis, this argument must defeat itself. If it be granted that either form may be derived from the other directly, by degeneration or otherwise, then, wherever it occurs it may have been so derived.

I have repeatedly insisted, both for myself and others, that because none of our problems in evolution are, as yet, capable of mathematical presentation and proof, we are not justified in stating any of our opinions or conclusions dogmatically or, in effect, writing Q.E.D. after any of them. I may, therefore, perhaps be permitted to record a protest against the presentation of opinions ("restorations") as though they were facts. This practice imposes upon readers the necessity of being constantly on the alert, lest they be misled into accepting those opinions as factual evidence, and calls for an irksome degree of concentration in the reading.

The Homology of the Crossopterygian Metapterygoid Bone.

An extraordinary confusion has resulted from the application of the designation "epipterygoid" to a certain bone in the wall of the cranial cavity of fossil amphibians and on the palatoquadrate of certain fossil fish. Säve-Söderbergh (1936, p. 145) wrote:

"The extension of the epipterygoid ossification in *Lyrocephalus* to include both basal, ascending and otic processes of the palatoquadrate throws a new light on the nature of the so-called metapterygoid of the Coelacanthids. It has already been shown by Stensiö that this *metapterygoid corresponds* to the *processus basalis, ascendens* and *oticus* of the palatoquadrate in Dipnoi and Tetrapods. We are now able to go further and say that the so-called metapterygoid of the Coelacanthids is the exact equivalent of a well-ossified *epipterygoid* of a Labyrinthodont. And even if it is probable that the bone discussed arose independently in the two groups by fragmentation of a continuous palatoquadrate ossification, it is evident: (1) that the

bone discussed of the Coelacanthids is much more closely comparable to the epipterygoid of the Tetrapods than the metapterygoid of the Actinopterygii; (2) that the presence of such *exactly comparable* bones is evidently due to very closely *comparable mechanical* conditions in the two groups, indicating a close relationship. Accordingly, it seems more correct that the bone discussed be called the epipterygoid also in the Coelacanthids."

So much of this quotation is so utterly at variance with generally accepted belief, that the absence of argument or evidence in support of its astonishing statements makes one wonder whether it is not entirely due to careless terminological inexactitude. It cannot, however, be dismissed so lightly. To begin with, his so-called epipterygoid (ept. fig. 5) is *probably* a prootic ossification, and *possibly* a predeterminate alisphenoid bone.

It will have been noted that in the above quotation he states that the epipterygoid ossification of *Lyrocephalus* includes not only the ascending process, but all three processes. He then states that the metepterygoid of Coelacanths has been shown by Stensiö to correspond to all three processes of the palatoquadrate of Dipnoi and Tetrapods, and next states that this metepterygoid is the "exact equivalent" of an epipterygoid in a Labyrinthodont. This is, in effect, stating that the ascending process of the quadrate in this Labyrinthodont is homologous with all three processes in the Dipnoi and Tetrapods. But the Labyrinthodont is itself a Tetrapod!
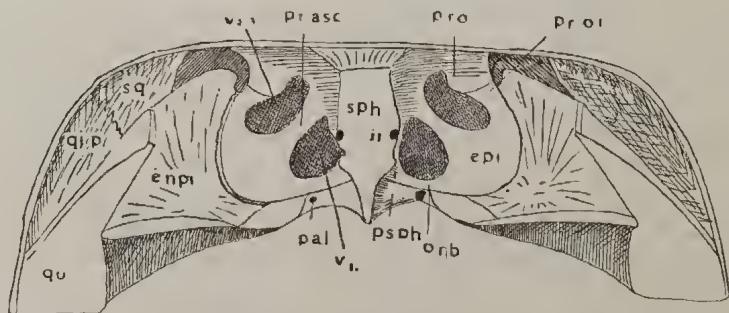

Fig. 5.—Lyrocephalus euri, Neurocranium and palatoquadrate, with the anterior part of the skull cut away (from Säve-Söderbergh, 1936).

The exact comparison of the quotation is based upon the supposed participation of the metapterygoid in the formation of a cavum epiptericum in the fish, and on the assumption that in the fishes in question the palatoquadrate was suspended from the skull by the metepterygoid alone.

The discovery of the complete and perfectly typical hyomandibular in *Megalichthys* and in *Latimeria* completely disposes the latter assumption, and with it the "closely comparable mechanical conditions."

It is, of course, well known that the palatoquadrate is attached posteriorly in all amphibians, except the Coecilians, by basal, otic and ascending processes. In the Coecilians only the ascending process is present. It is equally well known that the processus ascendens is present in embryonic stages, of all reptiles, and persists as an

independent "epipterygoid" bone in Lacertilia, Rhyncocephalia and some few other reptiles.

Unfortunately, this bone was confused with the alisphenoid bone of the Crocodilia and Cynodontia, so that this and the alisphenoid bone of some amphibians came to be designated epipterygoid. Kesteven (1918, 1926 and 1941) pointed out that whilst the bone in the Cynodonts was pretty certainly homologous with the alisphenoid of the Mammalia it was not homologous with the epipterygoid bone.

Be that as it may, the fact is that any bone in the side wall of the cranial cavity of an amphibian or a reptile may be designated "epipterygoid" only if it be deemed to be homologous with the processus ascendens quadrati. Säve-Söderbergh is not alone in describing on the palatoquadrate of fishes and in the side wall of the cranial cavity of certain amphibians an "epipterygoid bone"; a processus ascendens quadrati; which has, attached to it, ascending, basal and otic processes.

In view of the presence of the ascending process as one of the attachments of the palatoquadrate in all recent amphibians and in so many reptiles, we are surely simply compelled to regard it as an inherited feature. Further, since all three processes are present in all recent Urodela, Anura and Dipnoi, they, too, must be regarded as having been inherited from the common ancestor. If these be deemed reasonable assumptions, then it would seem to follow that primitive amphibians also had these same three processes. If not, whence came they in all the recent forms?

Whatever be the answer to the last question it is quite wrong to designate any structure the epipterygoid bone, unless it be equated with the processus ascendens quadrati.

Stensiö, Säve-Söderbergh and Watson all fail to compare the palatoquadrate arch of the Crossopterygians with those of fishes. The comparison is attempted here, and since illustrations convey shape and relations better than words the palato-quadrate arches of *Wimania, Macropoma, Lepidosteus, Salmo, Epinephalus* and *Latimeria* are pictured below (Fig. 6). It is surely quite clear that the only differences between these specimens are those due only to variation in the length and width of the component bones. The close resemblance of Smith's description and illustrations of the bones in *Latimeria* to those of the fossil forms justifies confidence in the correctness of the descriptions of the palaeontologists. These are fairly certainly, not coincidental resemblances. The bones are the same in the fossils and in the living forms.

It may be concluded that the metapterygoid bone of the Crossopterygians is not merely homologous with the bone of the same name in the recent fish, it *is* that bone.

THE PALATO-PTERYGOID PORTION OF THE QUADRATO-PALATAL ARCH

Romer (1937) offered an exceedingly interesting "working hypothesis" which, he says, is far more consistent with known palaeontological facts than those based primarily on embryology, which are now current. It is that in the primitive gnathostome the upper end of the maxillary and upper ends of the rest of the arches were fused to the skull.

This suggestion offers a very simple explanation for, and is supported by the cartilaginous continuity of, the anterior end of the palatoquadrate and ethmoid, which has been observed in some Elasmobranchs and Teleostomes, most Urodeles and all Anurans.
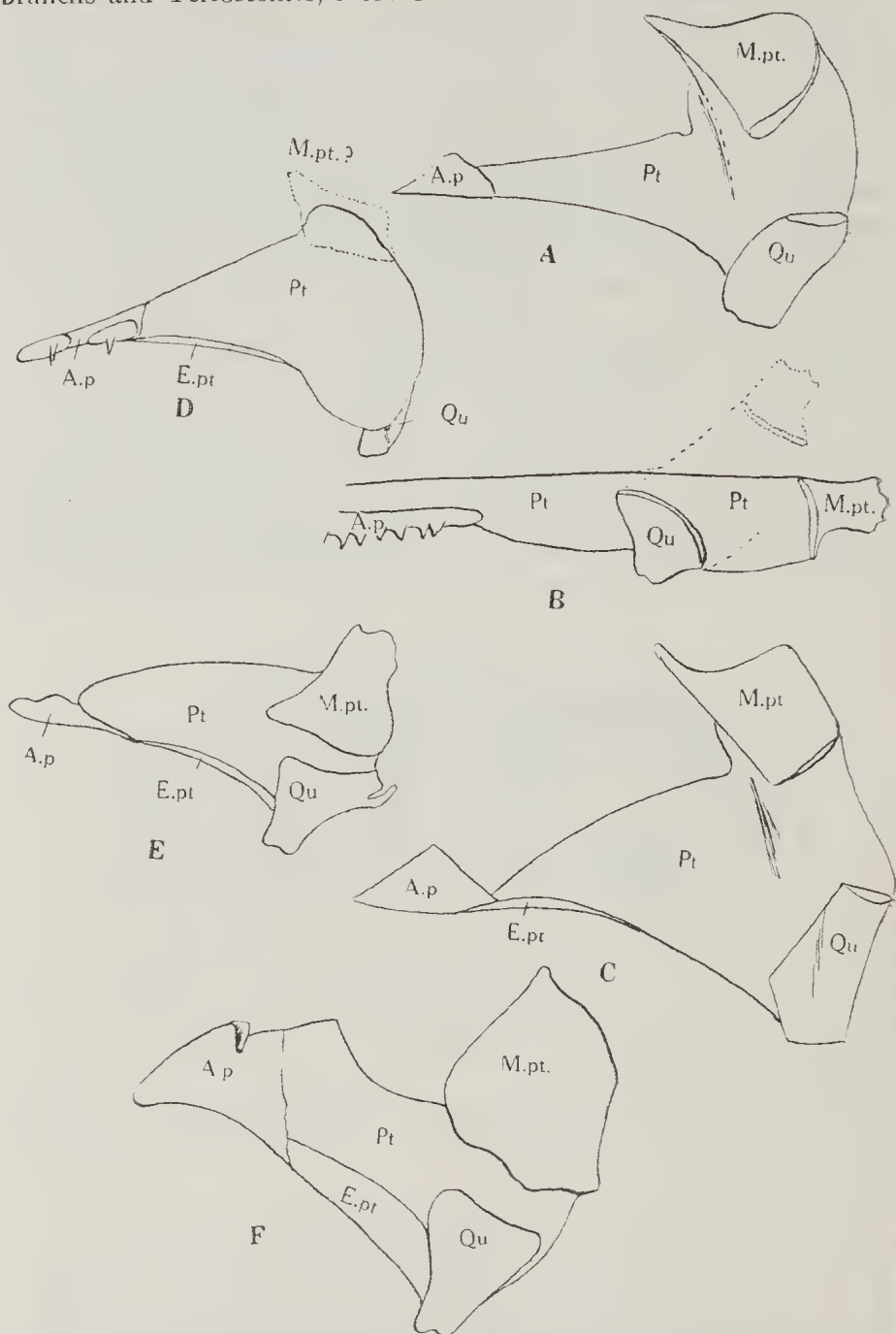

Fig. 6.—Palatoquadrate arches of:—A. Wimania, from Stensiö, B. Lepidosteus, from W. K. Parker, C. Latimeria, from Smith, D. Macropoma, from Watson, E. Salmo and F. Epinephalus.

It also offers a very simple explanation for the origin of the palato-pterygoid portion of the arch, and one more understandable than that generally accepted at present. The present belief is that the upper end of the arch is at the attachment to the skull behind, and the pterygoid process is deemed to be a secondary anterior growth. If Romer's suggestion is correct, then the upper end of the arch must be the anterior end, so commonly attached to the ethmoid. The palato-pterygoid portion would be regarded as the body of the original half-arch, and the quadrate and its processes of attachment would all be deemed to be secondary developments, in response to the mechanical need of firm fixation of the jaw joint, and the efficient development of the joint itself.

This explanation of the origin of the anterior portion of the palato-quadrate arch, granted that Romer's suggestion is correct, is not only a very simple one but it is supported by the mechanical factors which may reasonably be thought to have been operating. The current theory is based entirely on embryological evidence and is devoid of any mechanical explanation; nor does it explain why the anterior end of the process is so commonly continuous with the ethmoid.

It may be said that in a study of the cephalic musculature of the Elasmobranchii, the serial homology of the muscles of the branchial, hyoid and mandibular arches can only be understood on the assumption that the palato-pterygoid process is, itself, the upper half of the Maxillo-mandibular arch. (*Vide* Vetter 1874, 1878, Edgeworth 1935, Lightoller 1939, Kesteven 1942-45.)

Section III

The most convincing presentations of the case for the crossopterygian origin of the Tetrapods were the earlier contributions. These were based entirely upon the various features wherein the fossils clearly resembled the primitive amphibians. The most important evidence was that provided by the Upper Devonian fish, *Eustheno-pteron*. In fact, it is almost true to say that the whole case rested upon the marked similarity of certain features in the dermal shield and palate of this fish to those of the Embolomeri, primitive amphibians from the Coal Measures. The case has, since then, been further strengthened by the resemblances of the Ichthyostegidae, Upper Devonian amphibians, to *Eusthenopteron* and some of the other Devonian and Carboniferous Crossopterygians.

Although palaeontologists have interpreted the better preserved neurocrania of these fossil fishes as supporting the crossopterygian origin of the tetrapods, the fact remains that these are essentially the neurocrania of fish, and, as a matter of fact, bear very little resemblance to those of the primitive, fossil, amphibians.

Although the mutual resemblances of the dermal shields and palates of the primitive fishes and amphibians does justify a belief in the accepted theory, the evidence is far from convincing. A critical examination of the facts available leads to the belief that the dawn of the Tetrapoda antedated the appearance of the Crossopterygians and took place in Lower Devonian times or earlier.

The earliest known Crossopterygian is apparently *Porolepis*, which appeared in the Lower Devonian. Unfortunately, nothing is known

of its palate beyond the fact that the parasphenoid bone extended far forward, as in other members of the Rhipidistia, and that there was a tooth-bearing premaxilla. The evidence is scanty, but, as far as it goes, it suggests very strongly that the palate was similar to that of the Crossopterygia generally.

The Dipnoi and the Ichthyostegidae appear together, in point of time, in the Upper Devonian. There is no doubt that the latter were tetrapods, that in fact they were amphibians. There is no reason to believe that the Devonian dipnoans differed in any important respect from the recent forms, and the work of Kesteven (1931, a and b, 1942-45) and Kerr (1932) should have removed any doubt that they are primitive amphibians also.

There were, then, two distinct tetrapod types existing in Devonian times, and they must have been derived from an earlier ancestor. There is a general agreement that these two primitive tetrapods were derived from a common stock. It is obvious that the Ichthyostegids and the Dipnoans cannot have been derived from contemporaneous Crosso-pterygians, and, therefore, notwithstanding the many features of similarity, we must look elsewhere for the common ancestor of these two earliest tetrapods.

Before proceeding further it would be well to briefly review the features of similarity between the Ichthyostegids and the Dipnoans.

Säve-Söderbergh (1932, p. 98) wrote:—"in certain characters *Dipterus* seems to be more nearly related to the Ichthyostegids than are the Crossopterygians. Thus, its dermosphenotic seems to have fused with the postorbital; on the right of the specimen figured the supratemporal has fused with the intertemporal, and finally there is is an unpaired central parietal, whereas in Crossopterygians there are only paired parietal elements." He then gives details of certain dif-ferences, and, later, continues: "There is, however, also in the palate one feature in common to the Dipnoans and Ichthyostegids, but not found in the Crossopterygians, viz., the median suture between the anterior parts of the entopterygoids."

The position of the two nares is another feature wherein the Ichthyostegids resemble the Dipnoans. It may be that somewhat similar nares are present in some Crossopterygians.

There is yet another, and very important, feature in which the two tetrapods both differed from the Crossopterygians. This is the absence of the hyomandibular as a component of the suspensorium. Although overlooked or neglected by palaeontologists, this is a feature wherein the Dipnoi, and presumably the Ichthyostegids, present a distinct and fundamental *advance* on the crossopterygian condition.

It is difficult to believe that these features of similarity could have arisen independently in the two tetrapods; therefore, it would seem that if either was derived from a crossopterygian ancestry, both must have been. Since all known Crossopterygians had hyoid suspension, it seems improbable that the tetrapods were derived directly from them.

The undoubted resemblance in the number and arrangement of the bones in the palate must be accounted for on the assumption that all three derived the palate from a common ancestor.

The resemblance of the palate of the Dipnoans to that of the Ichthyostegids is not obvious, but is recognisable once it is realised

that the differences are due to the *absence* of bones from the former. It is generally agreed that the peculiar character of the Dipnoan palate is due to extreme specialisation, which has resulted in the *loss* of the bones related to the palato-pterygoid portion of the maxillary arch. The bones which remain differ from the corresponding elements in the primitive amphibian palates, in size only, *not* in their relations to one another or to the base of the cranium (Fig. 7). The essential similarity of these bones is only partly disguised by the peculiar teeth on those of the Dipnoans, and this difference in the teeth should not be deemed of phylogenetic importance because we observe equally marked differences in the teeth of, relatively closely related Elasmobranchs.
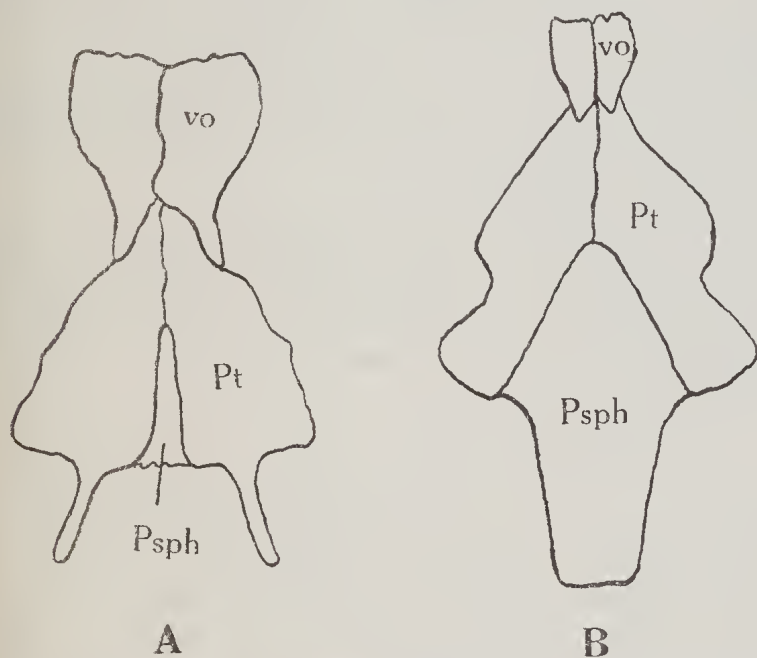

Fig. 7.—Two Dipnoan palates.

The important concept here is that the differences in the lateral parts of the palates is due to loss of bones from that of the Dipnoans. It will be observed that this is referred to as a concept, not as a fact; it is based upon an assumption. If that assumption is accepted as reasonable, then, one is emboldened to say that in their cranial osteology, the Ichthyostegids may almost be regarded as Dipnoans which have not lost the lateral elements of the palate, and in which the parasphenoid bone has undergone a further reduction towards that complete loss seen in the Sauria.

The reduction of the parasphenoid bone in the Embolomeri and the Ichthyostegidae is another fact which makes it difficult to believe that the Tetrapods have been derived from the Crossopterygians.

The Tetrapods can only be derived from the Crossopterygians through these two primitive groups of Amphibians. The whole of the arguments in favour of such an ancestry is centred on their mutual resemblances. In the reduction of the parasphenoid bone these two

groups have, as it were, progressed *beyond* the amphibian condition. In all other amphibians this bone is very extensive, covering nearly the whole of the ventrum of the neurocranium, and extending far forward beneath the ethmoid region.

If the Amphibians generally have been derived from the Crossopterygians, through either of these two groups of primitive Amphibians, then there must have been in all these others a return to the primitive fish condition in the size and importance of this bone as the covering of the base of the neurocranium. Such a complete reversal in an evolutionary change would be without parallel, and be difficult to explain or understand.

Another fact which should not be neglected in this connection is that all four groups of the Stegocephalians are represented in Carboniferous rocks, and not only is this so, but a primitive reptilian group, the Cotylosauria, are also of Carboniferous age.

There is little room for doubt that the Embolomeri and the Ichthyostegids were the amphibian group from which the Cotylosaurs were derived, it is difficult to believe that they also gave rise to the very dissimilar Stegocephalians.

After a very extended survey of the cephalic musculature, I could find no evidence, either in the embryology or the adult anatomy, of any teleostome ancestry for that of the Tetrapods. On the contrary it was found possible to derive it, through the branchiate Amphibians, the Dipnoans and Holocephali directly from the elasmobranchian condition (Kesteven, 1942-45). Lightoller was of the same opinion (1939).

To assert that the resemblances of all vertebrate palates are such that — they must have been derived from a common ancestor — would be to make one of those dogmatic statements which, I have said, we are not justified in making. But so general is the agreement on this matter that the statement would probably go unchallenged.

I have recently reviewed the arrangement of the bones in the palates throughout the whole of the various classes of the vertebrates, and found reason to believe that those of the tetrapods and the bony fishes were derived from an ancestry common to both, and that the former was not necessarily derived from the latter (Kesteven, 1947).

Reviewing the scanty evidence available, it certainly seems to point to the existence, in Lower Devonian or earlier times, of some, as yet undiscovered, ancestral form from which the Dipnoi, Ichthyostegidae and the Embolomeri were derived, and which itself was derived from an earlier ancestor common to it and the Crossopterygians.

This same scanty evidence also justifies the expectation that when discovered the Lower Devonian or Silurian, protetrapod will be found to have a palate made up of the number of bones found in the amphibian palates, with a large parasphenoid bone, and with the quadrate portion of the arch attached directly to the neurocranium, without any hyoid component in the suspension of the upper jaw arch.

From this protetrapod we may be permitted to believe that three distinct lines of evolution originated. The first was that leading to, and ending at, the Dipnoi. The second gave rise to the Stegocepha-

lians, and Euamphibia generally. The third gave origin to the Sauramphibia (Ichthyostegidae and Embolomeri), which, as the name suggests, gave rise to the Sauria.

THE DIPNOI.

Living Dipnoi are the most primitive amphibians known to us. Although they possess a few very characteristic fish features, they are very definitely not fish. Kellicot (1905) was the first investigator to carry out detailed work and to conclude from it that the Dipnoi are very closely allied to the Amphibia. In 1931 I published two papers in which the many points of resemblance of the Dipnoi to the Amphibia were detailed. In the following year, and quite independently, Kerr (1932) referred to a number of those features and added a few more, and he concluded (p. 421) that they constituted "together an assemblage of features which demonstrates irrefutably, the close relationship with the Amphibia *and the distinctness from the fishes.*" Dakin (1931) recorded that the body fluid of *Ceratodus* differed fundamentally from that of the fishes, and resembled that of the Amphibians. Recent investigations into the adult form (Kesteven, 1942-45) of the cephalic musculature, and its development (Edgeworth, 1923) in *Ceratodus* and other lung fishes reveals this to be very primitive. In the case of one set of muscles only was any resemblance found to the bony fishes, in six instances the resemblance is to the Amphibians. For the rest, the resemblance is to the Elasmobranchs.

Elliot Smith (1908) has two paragraphs which are of particular interest to the present discussion, in the summary of his description of the fore-brain of *Lepidosiren.*

"(1) If the features of the brain in the Dipnoi be considered as a whole, they will be found to approximate *much* more nearly to those of the Amphibia than to those of any other vertebrate.

"(9) The high state of development of the cerebral hemisphere in the Dipnoi gives us two alternatives from which to choose as to the relative positions of the Amphibians and the Dipnoi:—either the Amphibian hemisphere has passed through a state corresponding to that of the Dipnoi and has then undergone a secondary retrograde change, *or the Dipnoi are nearer to the main stream, which has led to the origin of the Amniotes.*" (The italics are mine.)

Confining himself, largely, to the dermal covering bones, Stensiö expressed the opinion that—"The study of the Coelacanths seems to help in throwing fresh light on the relationship of the Dipnoi and the Crossopterygians. According to our present knowledge, the latter, or forms very nearly allied to them, must be considered as ancestors to the Dipnoans, and must consequently be grouped close together with them from a systematic point of view. *There is no justification at all for separating the Dipnoi from the Teleostomes, as has hitherto often been done.*" (The italics are mine.) This statement is demonstrably quite wrong.

It is submitted that the tabulation below is, as Kerr said, an *irrefutable* demonstration of the close relationship of the Dipnoi and

the Amphibia. It is further submitted that such a preponderance of evidence of resemblances must be accepted as proving that the living Dipnoi are actually primitive Amphibians.

It may be pointed out that whilst there is room for difference of opinion as to the interpretation of characters No. 4 and 5 in the following table, the remainder are statements of fact, and do not introduce the personal factor at all.

TABLE 1.

RELATIONSHIP OF THE DIPNOI TO THE AMPHIBIA

The following dipnoan characters resemble the same characters:—	In the Amphibia	In the bony Fishes	In the Elasmobranchs	In None more than others
(1) The nearly complete cartilaginous nature of the skull.	+		+	
(2) The internal opening into the otocrane (Lateral cranial fenestra).		+		
(3) The autostylic and monimostylic suspension.	+			
(4) The nasal capsule.	+			
(5) The dermal roof pattern.				+
(6) The form of the frontal bone.	+			
(7) The form of the Squamosal bone.	+			
(8) The form of the forebrain.	+			
(9) The possession of internal nares.	+			
(10) The form of the heart.	+			
(11) The arterial system.	+			
(12) The venous system.	+			
(13) The fins.				+
(14) The form and function of the air bladder.	+			
(15) The structure and position of the glottis.	+			
(16) The possession of an epiglottis.	+			
(17) The possession of a true pelvic girdle.	+			
(18) The mating call of the male.	+			
(19) The body fluid.	+			
(20) The cytological character of every tissue in the body.	+			
(21) The form of the body.				+
(22) The mode of swimming.	+			
(23) The bones of the palate.				+
(24) The character of the scales.				+
(25) The Csv.1 Muscle.			+	
(26) The Csv.2 Muscle.			+	
(27) The M. interhyoideus.			+	
(28) The M. retractor mandibulae.	+			
(29) The Mm. interbranchiales.	+			
(30) The Mm. levatores arcuum branchialium.			+	

The following dipnoan characters resemble the same characters:—	In the Amphibia	In the bony Fishes	In the Elasmobranchs	In None more than others.
(31) The M. cucullaris.			+	
(32) The Mm. subarcuales.		+		
(33) The M. constrictor pharyngei.				+
(34) The M. coracomandibularis.			+	
(35) The M. coracobranchiales.			+	
(36) The M. pterygoideus.	+			
(37) The M. quadratomandibularis.	+			
(38) The general course of development.	+			
(39) The mode of the development of the external form.	+			
(40) The manner of the development of the two-chambered auricle.	+			
(41) The manner of the development of the amphibian characters in the arterial system.	+			
(42) The manner of the development of the amphibian characters in the venous system.	+			
(43) The development of the cerebral hemispheres.	+			
(44) The early form of the chondrocranium.	+			
(45) The development of the buccal cavity.	+			
(46) The form of pituitary involution.	+			
(47) The development of the flask glands.	+			
(48) The development of the cement organs.	+			
(49) The history of the palatoquadrate.	+			
(50) The development of the M. cucullaris.		+		
(51) The development of the M. retractor mandibulae.	+			
(52) The development of the other muscles of the head.			+	
(53) The development of outgrowths from the ductus endolymphaticus of the otocyst.	+			
(54) The cytology of all the embryonic tissues.	+			
(55) The development of true external gills.	+			
(56) The act of copulation.	+		+	
(57) The fact that the newly-hatched young must be permitted to rest with the mouth out of water, or they will drown.	+			

THE EVOLUTION OF THE TETRAPOD LIMBS.

Beyond doubt, the tetrapod limb has been evolved from some form of fin. The palaeontologists, with their view largely directed by the finger-posts of the bone-paved road they travel, have devoted their contributions to the attempt to decide what is the most likely way in which the bony segments of such fins as those of *Sauripterus* and *Eusthenopteron* may have rearranged themselves into the primitive limb pattern, such as that of *Eryops*.

Gregory (1935), and Romer and Byrne (1931), have given consideration to the effect of the attached muscles upon the rotation of the limb, but, so far as I am aware, no evidence has been produced by the palaeontologists that the musculature of the fin types selected as precursory to the limb type, was arranged segmentally along the length of the fin. In the living Crossopterygian *Polypterus*, and probably also in *Latimeria*, there is no such segmental arrangement of the muscle. In *Neoceratodus*, however, the muscle extends along the fins in a series of segments, in such wise as to permit of the differential movement of the segments of the fin upon one another (Fig. 8). It seems obvious that some such arrangement as this was essential as a prerequisite to the development of a jointed limb. The fins of the Dipnoi were of an extremely generalised type, such as may be imagined
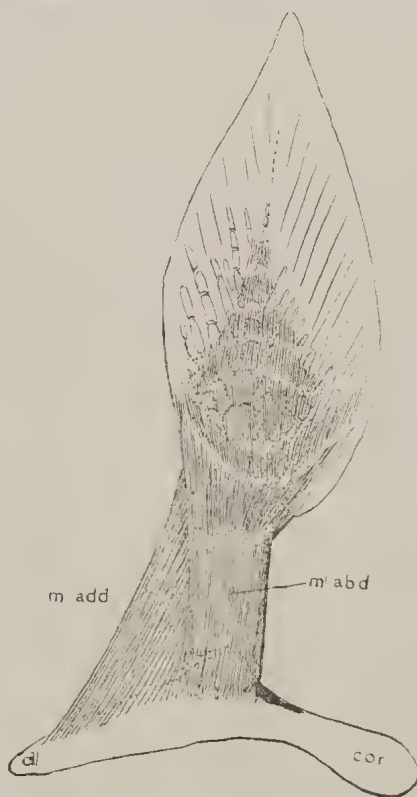

Fig. 8.—The Muscles of the Pectoral Fin of Epiceratodus. An external view of the superficial muscles. It will be noted that the superficial fasciculi extend across more than one joint but that, proximally, their deep portions extend across only one joint. The skeleton is shown in dotted lines.

to have been capable of variation, under the influence of this differential supply of muscles, and to have been capable of yielding, amongst these variations, the one which proved to be the starting point of the tetrapod limb.

Of course, this is not evidence that the tetrapod limb was derived from an archipterygium, but it must at least be conceded that the Dipnoi certainly possessed the one mechanical kinetic factor necessary for the evolution of the jointed limb.

The fact that *Neoceratodus* uses the pectoral limb to crawl clumsily out on to sloping rock to bask, is not evidence that it was used in the one way which would seem to have been most important to the production of a limb. *Periophthalmus* and a large number of the Gobiadae use the pectoral limbs in this manner a long way more efficiently than the Dipnoan does.

I have illustrated a dissection of the muscles of the fin of *Neoceratodus* which depicts the segmental arrangement of the muscles, and also the cartilaginous skeleton of the fin. I have not attempted to present drawings of hypothetical modifications of this fin, but it is obvious that its generalised form would permit changes to fit almost any series of modifications culminating in a primitive limb.

Conclusion

The natural classification of the vertebrate has been attempted by so many well-qualified men that to present still another classification calls, perhaps, for some justification.

It may be said of all recent attempts that they are based upon incomplete surveys of the facts which should be passed in review, and the present suffers from the same shortcoming. This is probably unavoidable. No one of us can possibly make himself sufficiently familiar with all the facts to undertake their evaluation himself. On the other hand it is submitted that an attempt to interpret the facts observed in a restricted field, but including all the vertebrate groups, by one who has devoted many years to the examination of those facts with that object in view, may be expected to advance the solution of the problem a little.

The field selected is the head and neck. During the past forty-odd years, the development and the anatomy of the head and neck of a very wide variety of representatives of every vertebrate group has been studied by the writer. In the course of that work it has appeared that too often investigators have accounted for similarities by assuming that they were coincidental or mere parallelisms, analogies, and not homologies, and so dismissed them.

The peculiar mixed characters of the Holocephali and the Sturgeon-like Chondrostei provide examples.

In A and B of diagram I below, characters 1 to 7 are outstandingly elasmobranchian, whilst characters 8 to 13 are outstandingly teleostoman. It can hardly be a coincidence that both the Chondrostei and the Holocephali combine so many of these characteristics. It seems that the only reasonable interpretation of the facts is that these 13 characteristics were present, actually or potentially, in the common ancestor of all four groups.

It is suggested that if these four groups were represented in numerical equality in the modern fauna, they would all have been given equal rank; and that the relegation of the two smaller to sub-groups was simply the result of their numerical inferiority and is not justified by their structure.

This concept permits the visualising of four distinct lines of differentiation at the dawn of the true fish epoch. The Plagiostoman, the Holocephalan, the Chondrostean, and the Teleostoman. Thus, we have four starting points for the evolution of the modern vertebrates.

If, however, we turn to the geological record, we find a group of Elasmobranchs, the Acanthodei, which seems to combine all the characters of the Chondrostei and Teleostomi, and we are enabled to reduce our "stem" type to three, and all three are Elasmobranchs. The plagiostoman root form presents only the outstanding characteristics of the modern Plagiostomes; omitting the Holocephali, with their autostylic suspension, and teleostoman type of branchial arrangement and opercular covering. The branchial arrangement of the Holocephali is, undoubtedly, an acanthodian feature; this suggests that the two groups are differential forms of a common ancestor.

Therefore, it is permissible to suppose that from some generalised fish form two main lines of evolution took definite form. The one was the Elasmobranchian. In this a primitive hyostylic suspension was retained, the gill clefts were left exposed, and the power to develop bone was more or less completely lost.

In the second group the gills were collected under an operculum and the power to form bone was retained and improved upon. In this group two main lines of change or specialisation soon manifested themselves. In the one a modification of the hyostolic suspension was perfected; in the other fibrous attachments of the palatoquadrate arch to the cranium posteriorly were converted into cartilaginous, and finally, bony unions and then articulations or fusions. These two are, of course, the Acanthodian and the Holocephalan. The Acanthodian root in turn gave rise to two different stocks. One of these, the Chondrostean, had inherited strongly the primitive hyostylic suspensorial tendency and combined this with the other characters of the Acanthodei. The other, the Teleostoman stock, however, perfected the modified hyostylic mode of suspension.

Turning finally to the Holocephalan stock we find ourselves in the presence of the most interesting combination of root-stock characters in the series. To begin with, we find the Elasmobranchian specialisations, very complete cartilaginous cranium and absence of bone; next we have the acanthodian type of branchial skeleton with its operculum, and finally we find Tetrapod suspension of the palatoquadrate without the utilisation of the hyoid.

A comprehensive review of the vertebrate cranium reveals that invariably it commences as a fenestrated basket and, sooner or later, it is completed alternatively by cartilage or bone. There is little doubt that cartilage is the more primitive tissue of the two. Therefore, whilst it is probably correct to regard the absence of bone in the modern Elasmobranchs as a specialisation in that there has been a complete loss of bone as a cranial building tissue, the entirely cartilaginous cranium is fundamentally a primitive condition. It is in this
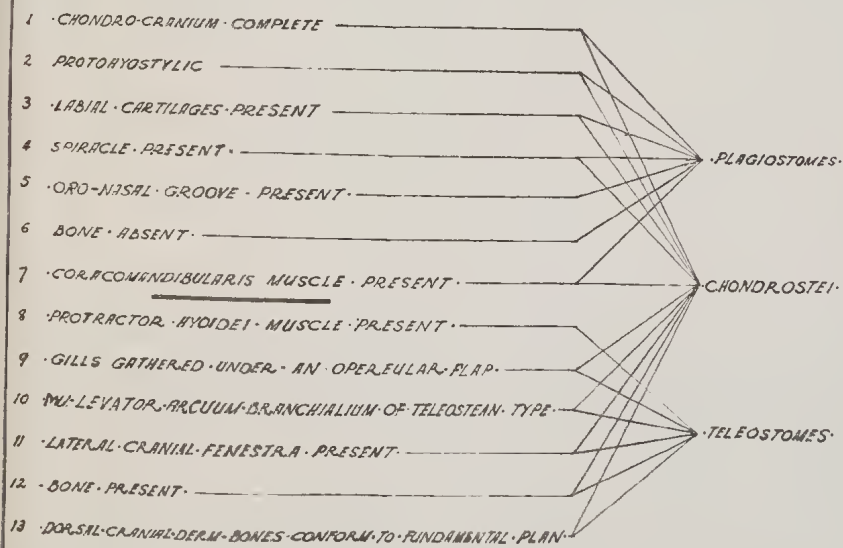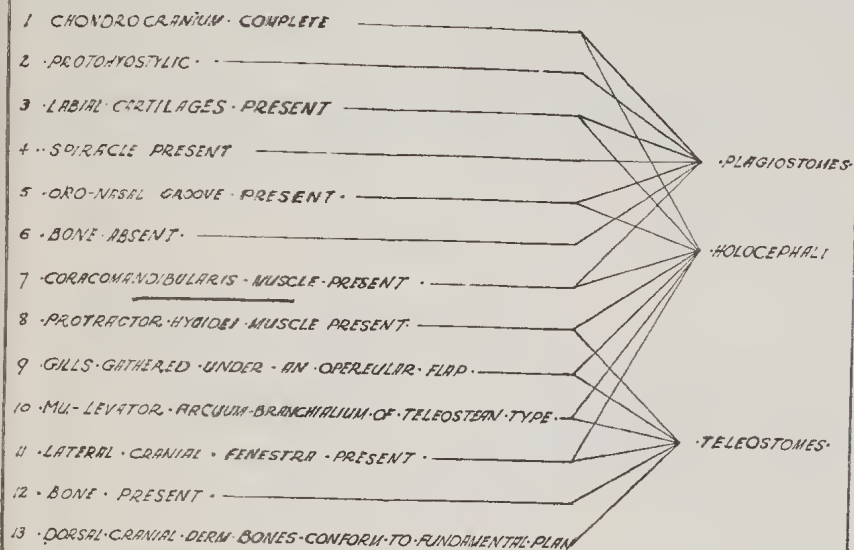
Diagram I.—A diagram designed to show the combination of different root-stock characters in the Holocephali and in the Sturgeon-like Chondrostei.

light that we should regard the cartilaginous cranium of the modern Holocephali. The absence of bone, however, is again a specialisation (comparable especially to the almost complete absence observed in Polyodon and Scaphyrhynchus) because the mesozooic Holocephali had more or fewer dermal bony plates related to the cranium. These modern members of the Holocephali are, of course, to be regarded as reflecting the general constitution of the root from which the Tetrapods have been evolved, and must also be deemed to have, themselves, departed in important particulars from that stock.

The first known definite tetrapod advance from the holocephalon stock is presented by the Dipnoi. Here we have a primitive Amphibian which retains a few very definitely "fish" characters. The outstanding resemblances to the Holocephali are the autostylic suspension, the lateral cranial fenestra (the wide opening into the otocrane from the neurocrane) and the branchial basket protected by its operculum.

It cannot, of course, be argued that the Dipnoi were themselves ancestral to the Tetrapods, but it should be clear from the tabulation of their tetrapod characters that they had advanced so far ahead of the Crossopterygians along the road to the Tetrapods that they cannot be regarded as having been derived from those fish. But, at the same time, the survival of the labial cartilages functioning as labial jaws in the Anura is such clear evidence of community of origin with the fishes that we must conclude they were both evolved from some earlier generalised form.

In diagram II I have made use of the term "osteichtys" for this generalised fish root-stock, and I have derived from it the Holocephali on the one hand and the Acanthodei on the other. From the Acanthodei, I derive the Chondrostei, which are to be regarded as a terminal type, and the Crossopterygii, which are to be regarded as the root-stock for all the rest of the bony fishes. From the Holocephalon root-stock I derive the Tetrapods.

Almost from their first appearance the Amphibians, which preceded all other Tetrapods in the Geological record, present themselves in three very distinct types, the Dipnoi, the Embolomeri, and the Labyrinthodont Amphibians. These may be interpreted as three divergent stocks which have evolved from the Holocephalon stem. The Dipnoi must be regarded as a persistent terminal group.

The Embolomeri and Ichthyostegidae may be united under the designation of Sauramphibia, to indicate that they must be regarded as the root-stock of the Saurians and higher Tetrapods generally, whilst the remainder may be designated Euamphibia. These last are all characterised by the retention of the undivided parasphenoid bone of the Fishes and are represented in the modern fauna by the Anura, Caecillia, and Urodela.

The Dipnoi probably are more closely related to the Sauramphibia than to others (Vide quotation from Elliott Smith, p. 127). Their exceedingly simple palate presents us with the simplest form of the divided parasphenoid bone. The deletion of most of the other bones of the upper jaw and palate must be regarded as the outstanding specialisation of this form of the primitive amphibian stock. The loss of bones is, in general, not phylogenetically significant; it is the form,

relation to one another and to the neurocranium, and the mode of development of the bones which are developed that reflect phylogenetic influence. The absence of the bones from the Dipnoan palate must be interpreted by one of two ways. Either the Dipnoi are so primitive that they come from ancestral stock in which palatal bones were as yet not developed, or they have lost all but a few of those bones.

Unfortunately, which of these interpretations we shall adopt must be decided by the personal equation. We have as yet no definite evidence on which to found a perfectly sound argument.
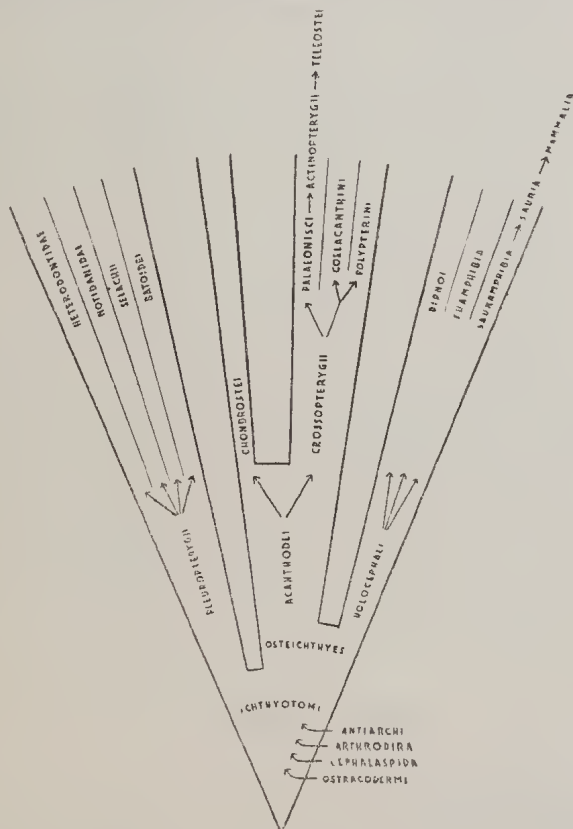

Diagram II.—A diagrammatic presentation of a natural classification of the Vertebrates.

It is a peculiar fact that the palaeontologists have either completely neglected the parasphenoid, commonly the largest contributor to the middle region of the palate in the fishes, or have been content to assume that an indefinite area of the basis cranii and a presphenoidal spur represented the bone, in their comparison of the Fish and primitive Tetrapod palates.

I have for long argued that the parasphenoid bones, so large and well-developed on the basis cranii of all fishes and modern Amphibians, is represented by the pterygoid bone in the Sauramphibia, the Dipnoi, and the rest of the Tetrapods. I have recently demonstrated, I believe irrefutably, that there is no parasphenoidal ossification on the base of the cranium in recent Sauria (Kesteven, 1940). It was

also demonstrated (Kesteven, 1941, 1942) that the so-called para-sphenoidal rostrum in the Avian skull is a cartilage bone and a true presphenoidal ossification.

The intrusion of the personal factor is unavoidable; it would be a weakness to try and disguise it, therefore — I find it difficult to believe that so important a bone in the ancestral forms should have no repre-sentation in the modern higher tetrapods. Especially, I find it difficult to understand how the parasphenoid bone of the Fishes can have been partly replaced by two *new* ossifications in the Dipnoi. Beyond question the posterior portions of the two palatopterygoid bones in the Dipnoi occupy, together, the exact position of the lateral wings of the parasphenoid of the fishes. I must continue to regard them as being the antero-lateral portions of that same bone, which has been divided into three. When first it was suggested (Kesteven, 1916) that the parasphenoid had persisted in two halves in the higher vertebrate, the suggestion that a single bone in lower might be homologous with paired bones in higher vertebrata was novel. Later, various observers thought to record the development of this bone on the base of various Saurians, mistaking "extraperichondral ossification" (Kesteven, 1942 A, p. 224) for membrane bone. Recently de Beer (1936), appar-ently without being aware of my earlier suggestion, proposed that the pterygoid of Ornithorhynchus be recognised as the lateral wings of the parasphenoid bone, and later de Beer (1937) extends this idea by suggesting that the dorsal component of the mammalian pterygoid is the homologue of the same lateral wing of the parasphenoid.

Returning to the question as to how we shall regard the paucity of bones in the Dipnoan palate. If the palatopterygoid bones in that palate are to be regarded as the advanced, tetrapod form of the parasphenoid bone, it appears to follow that we must conclude that the paucity of other bones is the result of loss, and not of primitive absence.

Final conclusions are, of course, presented in the last diagram.

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